STUDIES OF FOOD CONSUMPTION BY THE COW

by

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Preface

Studies on two different aspects of food consumption by the cow were carried out between 1960 and 1962 and are described in this thesis. The first consisted of an experiment designed to indicate whether or not dairy cows under the self-feeding, loose-housing system of winter management are able to consume silage to satiety. This study was suggested to me by my advisor, Mr. K. V. Runcie. The chromic oxide reference method was used as a basis for estimating the silage consumption of individual cows when self-feeding; its use was supervised by Dr. J. F. D. Greenhalgh. The results were presented to the winter meeting of the British Society of Animal Production in March 1962.

The second study was of the regulation of food consumption by the cow. Unlike the first, it was not undertaken with a view to providing information of immediate significance to agricultural practice; rather it was intended to enlarge our understanding of the physiology of the cow. I wish to acknowledge the stimulating discussion I had with Dr. D.G. Armstrong of the Hannah Dairy Research Institute at the outset and for the specific suggestion of an all-concentrate diet.

I wish to thank Professor S. J. Watson for the facilities he made available to me for the purpose of carrying out these studies.

Mr. K. V. Runcie and Dr. J. F. D. Greenhalgh, in addition to the specific help and suggestions referred to above, helped and advised me on numerous occasions throughout the course of

both these studies. I am greatly indebted to them.

I wish to thank Mr. A. King and his staff for their help in managing the experimental animals and Mrs. M. Jones for analysing milk samples.

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I am particularly pleased to acknowledge the constant encouragement and help of my wife Pramila.

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Part One

A Comparison of Silage Consumption of Dairy Cows Self-feeding and Individually Hand-fed

Introduction

It is well established that raising the level of grassland output constitutes an important opportunity for many farmers to increase their profits from dairying (Grassland Utilisation Committee, 1958). These farmers typically make limited use of grass or conserved forage and rely on more expensive concentrate feeds for most or all of the production ration. The way in which greater profits can be realised depends upon how the additional output is used (Ministry of Agriculture, Food and Fisheries, 1960). The dairy herd can be expanded, the level of concentrate feeding remaining unchanged. This alternative increases profits per acre of land devoted to dairying which may be particularly desirable on small farms. On farms with little or no capital with which to expand herd size, the additional output of grass can be used to replace concentrates in the ration.

In the case of the latter alternative, the maximum advantage from increased grassland output is secured by allowing lactating cows fresh and conserved grass ad libitum throughout the year. With skilful management of grass and cows to ensure maximum intakes of digestible dry matter at all times, the scope for obtaining profitable increments of milk yield from concentrate feeding is not large. During most of the grazing season the response of milk yield to supplementary concentrate feeding is small and is usually not profitable owing to low summer milk prices (Burt, 1957). During the winter many farmers using this

system feed their cows, on the average, only about 2 pounds of a low-protein concentrate mixture per gallon of milk produced (Dawkins, 1960; Holmes, 1961).

An important requirement for the successful operation of this intensive grassland system of dairying is that lactating cows achieve maximum voluntary intakes of available forage at all times. During the summer this can be met in efficient systems of grazing and in zero grazing. Since silage making forms an integral part of improved grassland management, silage is the main winter forage in this system. The self-feeding of this silage is becoming increasingly popular (Milk Marketing Board, 1962) because it eliminates the trouble and expense of handling the silage. Self-feeding, however, presents the cow with difficulties not encountered in grazing. She must take turns with the others at the feeding face and often actively fight for a place to stand and eat. She must pull the silage she eats from a densely packed mass. It is reasonable to inquire, therefore, whether or not all cows are able to achieve maximum voluntary intakes of silage when self-feeding. A report of such an inquiry forms this first part of the thesis.

Experimental Method

The consumption of silage by self-feeding cows, like the herbage intake of grazing animals, cannot be measured directly. For this reason there is no precise information about consumption with this method of winter feeding. The few estimates available (Hodges and O'Conner, 1960; Turner, 1953) have been calculated from the measured volume and density of silage consumed and the number of cow-days of feeding obtained. This method is easy and useful in planning farm operations, but is hardly suitable for assessing the nutritional aspects of self-feeding.

In this experiment, a single reversal trial with two groups of five animals, the intake of silage dry matter by individual animals when self-feeding was determined by the use of chromic oxide as a marker in conjunction with estimates of dry-matter digestibility obtained with the animals of the opposite group hand-fed on the same silage. This method is not favoured in grazing studies because of the difficulty of obtaining material for hand-feeding similar in digestibility to that grazed. With forage-harvested herbage, however, and especially with the precautions taken in this experiment, there was not considered to be any possibility for self-feeding animals to select a diet with an average digestibility significantly different from that consumed by hand-fed ones.

The silo and silage

Photograph 1 gives a general view of the experimental silo. It was newly opened for this experiment. The silage was made

system feed their cows, on the average, only about 2 pounds of a low-protein concentrate mixture per gallon of milk produced (Dawkins, 1960; Holmes, 1961).

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Photograph 1. A general view of the experimental silo. Freshly cut silage for hand-feeding is being mixed on the silo floor before being weighed out in the feeding baskets.

Photograph 2. Hand-fed cows eating.

the material was dried at once at 100 degrees and the rest frozen, to be later contributed to period bulk samples. There appeared to be a slight loss of moisture from the frozen samples, amounting to about one percentage unit. The bulk samples were dried in the same way as the daily ones. In addition, their dry-matter content was determined by toluene distillation (Dewar, 1960). From the difference between the oven-drying and toluene-distillation values a correction factor, representing the volatile dry matter lost in oven drying, and amounting to 7.3 percent of the oven-drying value, was calculated and then applied to the individual daily values obtained by oven drying. The pH and nitrogen contents of the bulk samples were determined, respectively, by a "Pye" pH meter and the Kjeldhal method (selenium catalyst).

Experimental animals

Details of the experimental animals are given in Table 1. All were pregnant and not lactating. The two heifers, F-54 and F-55, had, respectively, one and two of their adult teeth. Cow 62 was very aggressive and, at the other extreme, cow 82 was very timid.

Table 1. Details of experimental animals

Group	Cow	Breed	Body Weight* lb.	Stage of Pregnancy	Previous Experience in Self-feeding
	F-54	Ayrshire (heifer)	932	6th month	No
	104	Ayrshire	1262	7th month	No
A	10	Ayrshire	1317	5th month	Yes
	53	Friesian	1307	6th month	No
	23	Ayrshire	1102	5th month	No

(continued)

	F-55	Ayrshire (heifer)	922	7th month	No
B	82	Friesian	1158	6th month	No
	62	Ayrshire	1108	5th month	Yes
	29	Ayrshire	1167	6th month	No
	43	Ayrshire	1133	5th month	Yes

*Averages of 8 weighings taken throughout the course of the experiment.

Faeces sampling and analysis

The experimental animals were each dosed daily at 8:30 AM and 4:30 PM with a capsule containing paper impregnated with chromic oxide (Corbett, Greenhalgh and McDonald, 1960) and supplying 7.63 ± 0.08 g. chromic oxide. During experimental periods, faeces samples of about one pint were taken directly from the rectum at the same times. They were bulked for each cow for each period. The chromic oxide content of the bulked faeces samples was determined by a method which was essentially that of Christian and Coup (1954). Calculated faecal dry-matter outputs were used, first to estimate digestibility coefficients with the hand-fed animals in each period, and second, along with these coefficients, to obtain estimates of silage dry-matter intakes of animals self-feeding during the same period.[x] The nitrogen content of the bulked faeces samples was determined in the same way as the nitrogen content of the silage. There was no difference between treatments in faecal nitrogen content (Table 2). Since faecal nitrogen content varies with the digestibility of the dry matter consumed and is, in fact, used as an index of digestibility in grazing studies (Lancaster, 1949), this lack of difference between treatments supports the original

* For an example of the calculations involved, see the Appendix, page 23.

Table 2. Nitrogen content of faeces, percentage of dry matter.

		Period I: Self-feeding (S)	Period II: Hand-feeding (H)	S-H
Group A	F-54	2.80	2.61	0.19
	104	2.75	2.70	0.05
	10	2.82	2.66	0.16
	53	2.50	2.67	-0.17
	23	2.75	2.59	0.16
	Total	13.62	13.23	0.39
	Mean	2.73	2.65	0.08

		Period I: Hand-feeding (H)	Period II: Self-feeding (S)	H-S
Group B	F-55	2.69	2.48	0.21
	82	2.88	2.59	0.29
	62	2.78	2.59	0.19
	29	2.67	2.54	0.13
	43	2.86	2.75	0.11
		13.88	12.95	0.93
		2.78	2.59	0.19

Mean nitrogen percentage:	2.66	for self-feeding
	2.71	for hand-feeding
Difference	0.05	
Standard error of the difference	0.035	

Note on the period differences in faeces and silage nitrogen contents:

	Period I	Period II	I-II	$\frac{I - II}{I} \times 100$
Faeces	2.75	2.62	0.13	4.7
Silage (Fresh)	1.84	1.78	0.06	3.3
(leavings)	1.70	1.60	0.10	

claim that self-feeding animals had no opportunity to select from the available material a diet different in digestibility from those hand-fed.

Behaviour recording

A record of the activities of each animal during one 24-hour period in each experimental period was obtained by the interval recording method, using 5-minute intervals.

Results

A summary of the results is presented in Table 3. There was no difference in mean daily dry matter consumption per animal between treatments. All animals were equally successful in maintaining their dry matter intakes when self-feeding (Table 4). The daily time an animal spent eating when self-feeding was not significantly less than when hand-fed. Nevertheless, considerable reductions were observed with timid animals, i.e., 53, 82 and F-55 (Table 5). The reductions with these animals resulted from decreases in the number of meals per day (Table 6) and decreases in the duration of each meal (Table 7). Since their consumption was not less when self-feeding, they obviously ate more rapidly. Significant period differences in dry matter intake and time spent eating were found, averages for both being significantly lower in the second period. Figure 1 shows the daily feeding patterns observed on the two treatments. The eating of the self-feeding animals was spread out more uniformly over the period of silage availability than that of hand-fed ones. There were no differences among animals in the relative distribution of eating time over this period in either treatment.

Table 3. Summary of experimental results.

Mean:	Self-feeding	Hand-feeding	Diff.	S.E. of Diff.
Silage dry matter consumption, lb./cow/day	18.2	18.4	0.2	0.37
Time spent eating, h./cow/day	4.5	5.1	0.6	0.43
Number of meals/cow/day	17.8	14.0	3.8*	1.65
Duration of each meal, min.	14.9	22.3	7.4*	1.65
Time spent loitering, h./cow/day	11.7	7.8	3.9*	0.49
Time spent lying, h./cow/day	7.8	11.2	3.4*	0.48
Number of lying periods/cow/day	10.2	6.7	3.5*	0.47

*Difference significant (Probability = 0.05 or less)

Table 4. Silage dry matter consumption

	Cow		Period I: Self-feeding (S)	Period II: Hand feeding (H)	S-H
Group A	F-54		14.7	13.9	0.8
	104		17.6	17.4	0.2
	10		21.4	19.3	2.1
	53		24.2	22.3	1.9
	23		18.2	16.7	1.5
		Total	96.1	89.6	6.5
		Mean	19.2	17.9	1.3
			Period I: Hand-feeding (H)	Period II: Self-feeding (S)	H-S
Group B	F-55		14.4	13.5	0.9
	82		22.4	21.2	1.2
	62		21.4	20.5	0.9
	29		17.3	13.0	4.3
	43		18.8	17.2	1.6
		Total	94.3	85.4	8.9
		Mean	18.9	17.1	1.8

Mean dry matter consumption, lb./cow/day: 18.2 for self-feeding
18.4 for hand-feeding

Difference 0.2
Standard error of the difference 0.37

Table 5. Time spent eating

	Cow		Period I: Self-feeding (S)	Period II: Hand feeding (H)	S-H
Group A	F-54		5.1	3.7	1.4
	104		5.3	5.4	-0.1
	10		6.0	5.2	0.8
	53		3.9	5.3	-1.4
	23		5.2	2.9	2.3
		Total	25.5	22.5	3.0
		Mean	5.1	4.5	0.6
			Period I: Hand-feeding (H)	Period II: Self-feeding (S)	H-S
Group B	F-55		5.8	3.3	2.5
	82		6.0	2.3	3.7
	62		5.4	4.4	1.0
	29		5.5	3.7	1.8
	43		5.8	5.3	0.5
		Total	28.5	19.0	9.5
		Mean	5.7	3.8	1.9

Mean time spent eating, h./cow/day: 4.5 for self-feeding
5.1 for hand-feeding

Difference 0.6
Standard error of the difference 0.43

Table 6. Number of meals

		Period I: Self feeding (S)	Period II: Hand-feeding (H)	S-H
	Cow			
Group A	F-55	20	11	9
	104	17	12	5
	10	22	10	12
	53	14	17	-3
	23	25	13	12
	Total	98	63	35
	Mean	19.6	12.6	7.0

		Period I: Hand-feeding (H)	Period II: Self-feeding (S)	H-S
	Cow			
Group B	F-55	15	17	-2
	82	16	13	3
	62	12	18	-6
	29	15	12	3
	43	19	20	-1
	Total	77	80	-3
	Mean	15.4	16.0	-0.6

Number of meals/cow/day: 17.8 for self-feeding
14.0 for hand-feeding

Difference 3.8

Standard error of the difference 1.65

Table 7. Duration of each meal

		Period I	Period II	
	Cow	Self-feeding (S)	Hand-feeding (H)	S-H
Group A	F-55	15.3	20.2	- 4.9
	104	18.7	27.0	- 8.3
	10	16.4	31.2	-14.8
	53	15.3	18.7	- 3.4
	23	12.5	13.4	- 0.9
	Total	78.2	110.5	-32.3
	Mean	15.6	22.1	- 6.5
	Cow	Hand-feeding (H)	Self-feeding (S)	H-S
Group B	F-55	23.2	11.7	11.5
	82	22.5	10.6	11.9
	62	27.0	14.7	12.3
	29	22.0	18.5	3.5
	43	17.9	14.9	3.0
	Total	112.6	70.4	42.2
	Mean	22.5	14.1	8.4

Duration of each meal, min.: 14.9 for self-feeding
22.3 for hand-feeding

Difference 7.4

Standard error of the difference 1.65

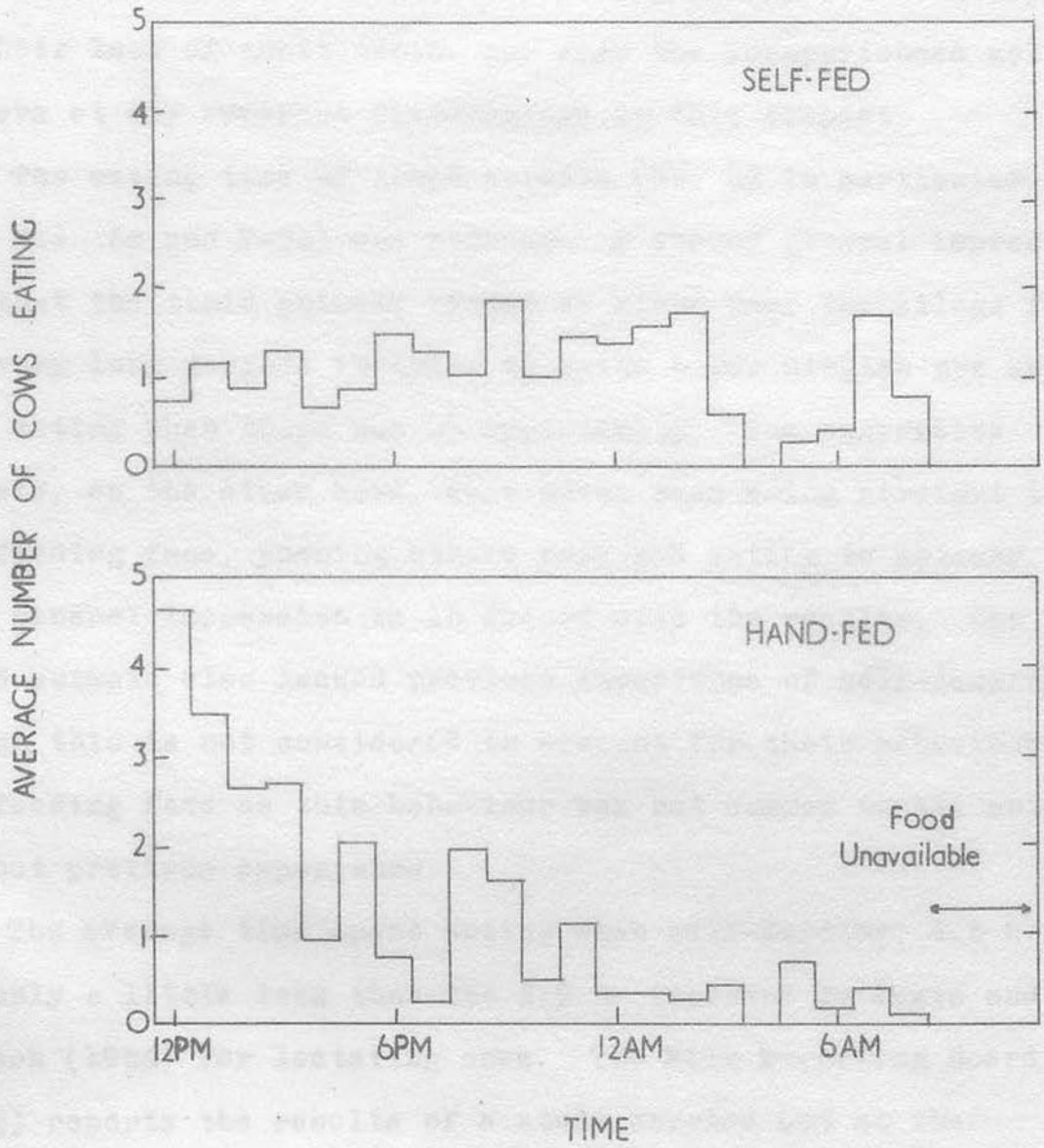
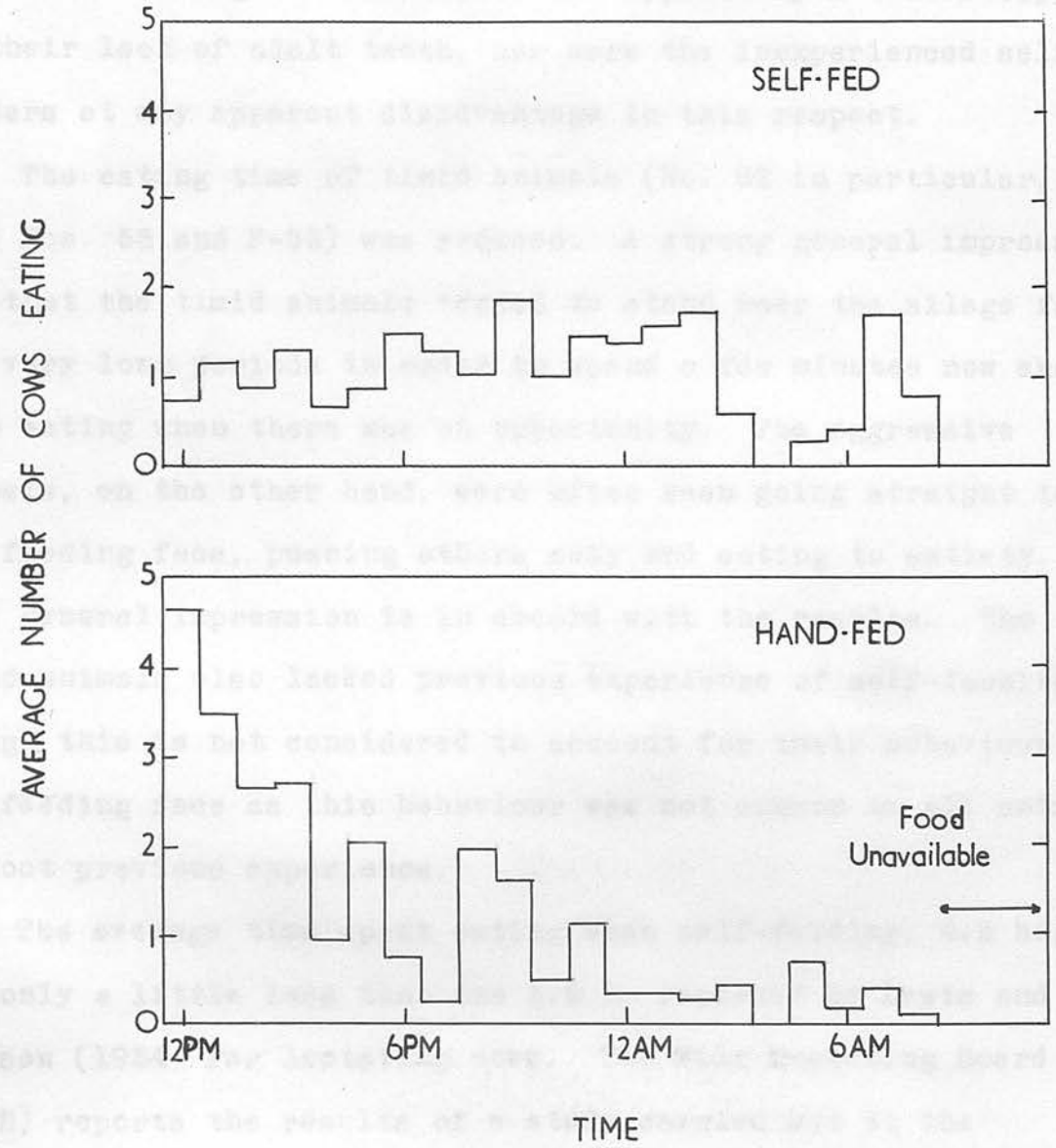


Figure 1. The average number of cows eating during each hour of the day. Data from both periods are combined.


SELF-FED
HAND-FED
Food
Unavailable
AVERAGE NUMBER OF COWS EATING
0
1
2
3
4
5
12PM
6PM
12AM
6AM
TIME

Discussion

All the animals used in this experiment clearly demonstrated their ability to achieve maximum voluntary intakes of silage when self-feeding. The heifers were apparently not handicapped by their lack of adult teeth, nor were the inexperienced self-feeders at any apparent disadvantage in this respect.

The eating time of timid animals (No. 82 in particular, but also Nos. 53 and F-55) was reduced. A strong general impression was that the timid animals tended to stand near the silage face for very long periods in order to spend a few minutes now and then eating when there was an opportunity. The aggressive animals, on the other hand, were often seen going straight to the feeding face, pushing others away and eating to satiety. This general impression is in accord with the results. The timid animals also lacked previous experience of self-feeding, though this is not considered to account for their behaviour at the feeding face as this behaviour was not common to all animals without previous experience.

The average time spent eating when self-feeding, 4.5 h., was only a little less than the 5.2 h. reported by Lewis and Johnson (1954) for lactating cows. The Milk Marketing Board (1962) reports the results of a study carried out at the National Institute for Research in Dairying; the mean daily time spent eating varied from 123 to 300 minutes, a range similar to that shown in Table 5.

The intakes of silage dry matter in this experiment were

18.3 lb. per cow or 1.6 lb./100 lb. liveweight. Moore, Thomas and Sykes (1960) report intakes of 1.6 lb./100 lb. for heifers (not pregnant) and 1.2 lb. for non-lactating cows on lucerne silage. These levels are lower than found with lactating cows in the experiments of Moore et al. (1960) and Hillman, Lassiter, Huffman and Duncan (1958) (1.8 and 2.2 lb., respectively). The animals in this experiment could reasonably have been expected to consume more silage after parturition. If this greater consumption had required longer eating times, the question of whether or not a timid cow like No. 82 could still have achieved maximum voluntary consumption arises. For this reason, it cannot be concluded from the results of this experiment that lactating cows, or at least all lactating cows, achieve maximum voluntary consumption when self-feeding.

No reason can be offered for the significant reduction in silage consumption and time spent eating from the first to the second experimental period. The existence of such differences suggests that a double reversal trial would have increased experimental precision (Brandt, 1938), but this would not be expected to have altered the conclusions drawn, at least with respect to silage consumption.

Summary

Ten dry, pregnant animals, divided into two groups, were used in a single reversal trial. When self-feeding the animals were allowed a one-foot width of the silage face each and when hand-fed they received material cut from a protected area of the same face. Estimates of faecal dry matter output, obtained by using chromic oxide paper, were employed to determine first, the dry matter digestibility for the hand-feeding treatment and second, in combination with this digestibility value, the dry matter intake when self-feeding. The activities of the animals were recorded by the interval recording method during one 24-hour period in each experimental period.

The animals consumed 18.3 lb. silage dry matter daily each (1.6 lb. per 100 lb. liveweight) and there was no difference between treatments. Timid cows, heifers and inexperienced self-feeders were as successful as others at self-feeding. Animals spent about 5 hours per day eating and there was not a significant difference between treatments. When self-feeding they ate more frequently (17.8 vs. 14.0 times per day), but the duration of each meal was less (14.9 vs. 22.3 minutes). Eating time on the self-feeding treatment was spread more uniformly over the day than on hand-feeding.

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Appendix

An example of the calculations involved in the estimation of silage dry-matter intakes of cows self-feeding

For Period I silage dry-matter digestibility coefficients were estimated with cows of Group B (hand-fed). The calculations for F-55 are:

Mean daily silage D.M. intake, lb. = Mean daily D.M. offered, lb. − Mean daily D.M. refused, lb.

" = 18.0 − 3.6

" = 14.4

$$\text{Mean daily faeces D.M. output, lb.} = \frac{\text{Cr}_2\text{O}_3 \text{ content of two capsules, lb.}}{\frac{\%\ \text{Cr}_2\text{O}_3 \text{ in faeces ash}}{100} \cdot \frac{\%\ \text{ash in faeces D.M.}}{100}}$$

$$\text{"} = \frac{2 \cdot 0.0168}{\frac{4.93}{100} \cdot \frac{14.23}{100}}$$

" = 4.63

$$\text{D.M. digest., \%} = \frac{\text{D.M. intake} - \text{D.M. output}}{\text{D.M. intake}} \cdot 100$$

$$\text{"} = \frac{14.4 - 4.63}{14.4} \cdot 100$$

= 66.8

For the five cows of Group B the mean silage dry-matter digestibility was 69.8 percent (S.E. of mean, 1.1 percentage units).

The silage dry-matter intakes for cows of Group A in Period I were then calculated. The calculations for F-54 are:

$$\text{Mean daily faeces D.M. output, lb.} = \frac{\text{Mean daily D.M. output, lb.}}{\frac{1 - \text{D.M. digestibility, \%}}{100}}$$

$$\text{"} = \frac{4.45}{1 - 0.698}$$

" = 14.7

Part Two

The Regulation of Food Consumption by the Cow

Introduction

The means by which the adult, non-ruminant mammal maintains its body weight constant through time, or in other words, continuous energy equilibrium, have been actively investigated for several decades. As a result it has been established that the principal means under most conditions is by the regulation of food consumption or energy intake. The ranges of environmental stress within which this regulation effectively operates have been roughly defined, and it is known that outside these ranges energy expenditure is regulated, though often only after body weight has changed considerably from its usual level. Furthermore, it is well established that the physiological basis of this regulation consists of a number of specific nervous and humoral factors acting through an integrating centre in the central nervous system.

The purpose of the present study has been to examine the behaviour of the cow for evidence of a similar ability to regulate food consumption to maintain continuous energy equilibrium. The general approach has been the same as with previous studies of non-ruminant mammals.

Development of Hypothesis

1. The Regulation of Food Consumption by the Non-ruminant Mammal: a Review

The adult mammal tends to maintain a constant body weight. This reflects the constancy of water content and of dry-matter content separately. The constancy of dry-matter content, its characteristics and the means by which it is achieved, are reviewed in this section. At the outset, however, it is necessary to refer to the relationship between dry-matter content and energy balance and to describe the methods of measuring changes in dry-matter content.

Constancy of dry-matter content, as of water, is achieved by the regulation of both intake and output to achieve continual equilibrium. Unlike water, however, dry matter (at least the bulk of it, the organic matter) does not, except for the organic matter of urine, leave the body as such, but in the form of carbon dioxide and water, after undergoing oxidation. The rate of loss of body organic matter is determined by the body's rate of energy expenditure. Therefore, the dry organic-matter content (henceforth referred to simply as "dry weight") is linked with energy balance. In the following discussion the terms energy equilibrium and constancy of dry weight are used interchangeably, as are positive and negative energy balances and gains and losses in dry weight. It is recognised that an exactly constant relationship between energy balance and dry weight change over a range of dry-weight change may not obtain, that the material

composition and thus the relative calorific value of changes in dry weight may not be constant.

Gasnier and Mayer (1939) in their experiments with rabbits estimated the daily change in dry weight by means of the following relationship, all terms of which are in grams per day.

$$\Delta \text{ Dry weight} = \Delta \text{ Body weight} - \left\{ \begin{array}{l} \Delta \text{ Alimentary content of indigestible dry matter} \\ \qquad + \\ \Delta \text{ Body water content} \end{array} \right\}$$

Δ Dry weight includes the change in dry weight not only of the body proper but also the change in weight of potentially digestible dry matter in the alimentary tract. The change in weight of inorganic matter is included in Δ Dry weight, giving rise to a small error. The authors were also able, by means of indirect calorimetry, to express the daily change in terms of calories. Morrison (1956) estimated daily changes for rats in terms of calories by indirect calorimetry. Most investigators, however, use body weight change as an index of dry weight change. This is a simple but crude index. The random variations in daily water balance are so much larger than variations in dry weight as to obscure them completely; the coefficient of variation of daily body weight under constant environmental conditions falls between 0.5 and 1 percent for several species (page 67), whilst the variation in dry weight

accounts for only a fraction of this (Gasnier and Mayer, 1939--see page 27)(Taggart, 1962). The average daily change for a number of consecutive days, however, is closely related to the average daily energy balance (Taggart, 1962) and is a reliable index of long term change in dry weight (Mayer and Hagman, 1953d; Kennedy, 1950; Keys, Brožek, Henshel, Michelsen and Taylor, 1950). This is to be expected from the fact that water content is regulated and does not increase or decrease in amount, under most conditions, except in association with increases and decreases in dry weight.

The results of Gasnier and Mayer's experiments with rabbits are the clearest demonstration of the constancy of dry weight in a constant environment. Their 23 rabbits were maintained for 80 consecutive days at an environmental temperature of 18 to 20 degrees C. and a relative humidity of 85 percent. They had water and a food of constant composition ad libitum. The occurrence of daily dry-weight changes greater than 10 g. was about 1 in 10 (average weight of rabbits, 2900 g.). Further, the distribution of the daily changes around the modal change was not random; a change in one direction on any given day tended to be followed by a change in the opposite direction the following day. Thus dry weight oscillates around a constant amount; it is actively maintained at a preferred level. It should be added that the modal daily change need not be zero. In the case of young growing animals and in that of animals with developing obesity due to any cause (cf. page 32), the modal change is a positive value; the animal maintains not a constant dry weight but a constant rate of increase in dry weight. Dry weight oscillates

around a constantly increasing amount (Mayer, 1955b). When the young animal is fully grown and when the obesity has reached a static phase, the modal change falls to zero.

The regulation of food consumption

There is ample evidence that the constancy of dry weight is achieved under most circumstances by the regulation of food consumption so that energy intake continually balances energy expenditure. If energy expenditure increases due to reduced environmental temperature, physical exercise, lactation or increased basal metabolic rate, food consumption increases sufficiently to maintain energy equilibrium. Food consumption increases if the energy content of the food is reduced by the addition of indigestible bulk. Experiments in which this has been demonstrated are discussed here according to the type of treatment imposed on the experimental subjects. Unless otherwise stated, these subjects were adult, their body weights remained constant and food of a constant composition (and containing enough nitrogen and minerals to prevent any negative balances of these elements) was available to them continuously to ensure ad libitum consumption. The treatment effects discussed are those observed when the subjects had become adapted to the treatment; the immediate effect of most treatments on food consumption is to reduce it, while the long-term effect may be an increase or a reduction (Mayer, 1955a).

Temperature

During a further 80-day period, Gasnier and Mayer (1939) made their rabbits live at 30, 18 and 0 degrees and at 18 and 8

degrees after being shaved. In this way a range of energy expenditures was obtained. Daily dry-matter gain and loss were determined as before. The correlation between the two was very good over the entire range; as the rate of loss increased, intake increased to maintain dry weight. This regulation of food consumption is considered by the authors to be the result of two regulatory processes. First there is the process which regulates daily energy intake in accordance with expenditure. This regulation is not perfect; small daily imbalances occur, resulting in small changes in dry weight. These imbalances are not random in occurrence. One day's imbalance tends to be offset the next day by an imbalance of the opposite sign (as was observed in the previous experiment under constant conditions). Thus there seems to be a second process which successively compensates for these errors in the day-to-day regulatory process. The authors also define and calculate parameters which describe how well these regulatory processes function; these are precision, reliability, sensitivity and rapidity. Another important fact brought out by this study is that an animal's dry weight does not necessarily remain constant with an increase in rate of energy exchange. Each time the rabbits were introduced to a lower temperature there was an initial slight increase in dry weight which was then maintained once equilibrium was re-established. Such changes in dry weight occur with some other treatments as well.

Donhoffer and Vontoyky (1947) found that food consumption increased in white mice at low (10 to 11 degrees) and decreased

at high (29 to 33 degrees) environmental temperatures. These changes were due almost exclusively to an increase or decrease in the consumption of a carbohydrate-rich food, free-selection of foods rich in either carbohydrate, protein or fat being permitted.

Kennedy (1952-53) found that the food consumption of both lactating and non-lactating rats increased to offset increased heat loss at 34 degrees F.

Exercise

Mayer, Marshall, Vitale, Christensen, Mashayekhi and Stare (1954) exercised mature rats, which were accustomed to a sedentary existence, on a treadmill for daily periods of increasing length. The rats had previously been trained to run on the treadmill. For low durations of exercise (20 min. to 1 hr.) there was no corresponding increase in food consumption; in fact, it decreased slightly but significantly. Body weight also decreased. For longer periods (1 to 5 hr.) food consumption increased linearly and weight was maintained. For still longer periods the animals' food consumption and body weight decreased. These ranges of activity are termed by the authors sedentary, normal and exhaustion. Both the sedentary and the exhaustion ranges are considered non-responsive ranges with respect to food consumption.

Mayer (1955c) also demonstrated the existence of a sedentary, non-responsive, range of activity in man. He estimated the daily energy intakes and expenditures of groups of men in West Bengal engaged in occuptions which required varying amounts of physical exertion, ranging from the tending of a stall in the bazaar to the heaviest types of manual labour. The energy values of food consumed was calculated from chemical analysis and standard

energy values for carbohydrates, proteins and fats. A portable respirometer was used to determine indirectly rates of energy expenditure for various activities and these were then used in conjunction with records of activities to estimate daily expenditure. Calorie intake decreased linearly with decreasing expenditure over only part of the range examined, from the highest levels of expenditure (labourers) to near the middle of the range (active clerks and mechanics); from this point decreasing expenditure was not accompanied by decreasing intake, rather, intake increased rapidly, until, at the sedentary end of the range, the intakes of the almost immobile stall-holders equalled those of the heaviest manual labourers. The stall-holders and clerks were thus living in a sedentary range in which intake no longer responds to further decreases in expenditure and the individual accumulates fat, i.e., increases in dry weight. This was clearly indicated by the continuous increase in body weight with decreasing expenditure over the lower half of the range.

The existence of this sedentary, non-responsive, range of energy expenditure readily explains the fact that immobilisation (or very restricted activity) of animals (Gasnier and Mayer, 1939; Ingle, 1949; Mayer, 1953a) and of men (Greene, 1939) causes an abnormal increase in body weight, obesity. Farmers for ages have taken advantage of this fact by penning pigs for fattening. Most obese people live in this sedentary range (Bruch, 1940; Rony, 1940; Bronstein, Wexler, Brown and Halpern, 1942; Graham, 1947; Tolstrup, 1953) and the primary aim in the therapy of obesity is to move them out of this range through regular exercise (Mayer, 1955b).

The development of obesity due to immobilisation does not mean that the regulatory process ceases to function in the non-responsive range. In experiments where obesity resulting from immobilisation has been carefully followed, two distinct phases are observed (Mayer, 1955b), a "development phase" characterised by an increasing body weight (a positive modal daily change in dry weight) and a "static phase" characterised by a constant but larger body weight (modal daily change is zero). At the onset of the static phase food consumption decreases until energy equilibrium is re-established. The stability of weight in the static phase, under constant environmental conditions, is similar to that in the non-obese individual (Kennedy, 1950; Mayer, 1955a; Nadal, 1954). Obese adult people who again eat to appetite after periods of restricted food consumption and consequent weight loss, or who slip back into the previous sedentary mode of life after a period of regular exercise and weight loss, invariably return to their preferred (obese) weights (Bowser, Trulson, Bowling and Stare, 1954). Similarly, obese children quickly slip back into their former abnormal height-weight growth channel (Bruch, 1955; Stuart, 1955).

It is obvious, therefore, that the obese individual has a preferred weight and that he actively maintains this larger preferred weight just as he did his previous smaller one. The parameters of the regulation (Gasnier and Mayer, 1939) can be calculated (Mayer, 1955a). The net effect of immobilisation, or very sedentary living, is to shift upwards

the preferred body weight.*

It should be added that the magnitude of the effect of a given degree of immobilisation will vary widely among species, strains and individuals. Pigs of different breeds fatten at differing rates and reach differing degrees of fatness. Gasnier and Mayer (1939) found a ten-fold difference in the rate of dry weight increase between two rabbits of the same sex and breed under identical conditions. Hereditary factors are obviously involved; "Constitutional factors determine the extent of this (non-responsive) range as well as the magnitude of the effect of immobilisation." (Mayer, 1955b).

A number of energy-balance studies have been carried out on human subjects under the conditions of variable daily energy expenditure encountered in normal living. Passmore, Thomson and

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*Much of the present knowledge about the regulation of food consumption in normal animals, non-obese as well as obese, has been obtained by the study of animals with experimentally induced obesity. If neurons of the ventromedial nuceli of the hypothalamus, which are thought to constitute a satiety centre (see page), are physically damaged (Kennedy, 1950 and 1952-53; French, Zighera and Mayer, 1955) or if they degenerate due to the action of injected goldthioglucose (Marshall and Mayer, 1954) obesity results. The positive energy balance in the development phase results, in the case of goldthioglucose obesity, from hyperphagia alone, whereas in obesity caused by physical damage it results from both hyperphagia and a reduction in voluntary activity.

The study of the hereditary obese-hyperglycemic syndrome in mice has also been very fruitful (Mayer, Bates, Vitale and Dickie, 1951; Mayer, 1953b; Mayer et al. 1954). This type of obesity, which is shown by individuals as well as strains, results almost entirely from a reduction in voluntary activity, i.e., a purposeful avoidance of activity where the opportunity for it exists; food intake is normal. In a common form of human obesity the positive energy balance is the result of reduced voluntary activity and not of overeating (Johnson, Burke and Mayer, 1956). Various types of obesity and their characteristics have been reviewed by Mayer (1955b).

Warnock (1952) estimated the daily energy intakes and expenditures of 5 healthy men over a period of 13 days, during 5 of which the subjects carried out tasks involving great energy expenditure. They found poor agreement between daily intake and expenditure; expenditure exceeded intake on active days and vice versa on inactive days. The overall balance was, however, near zero. Differences between initial and final body weights were noted, but could not be assessed owing to the shortness of the experimental period and the lack of water balance data.

Edholm (1961) reviewed a number of studies carried out in a similar manner on young men under military training in different climates and concludes:

1) There is no relationship between daily food intake and energy expenditure; as in the previous study, negative imbalances occurred on active days, positive on the succeeding inactive days.
2) Body weight can show marked fluctuations from day to day, probably due to water imbalance.
3) In spite of these two findings, over a period of a week or more, energy intake and expenditure are closely balanced and weight remains relatively constant.

Durnin (1961) reported the results of studies of six widely differing groups of people engaged in their normal daily routines. Daily energy intake and expenditure were estimated on seven consecutive days. With only 8 of the 69 subjects was daily intake significantly (positively) correlated with expenditure. Unlike the other studies with human subjects, however, there were

significant differences between the 7-day totals for intake and expenditure in a large number of the subjects (20 out of 69). In about half of these, intake exceeded expenditure. There was, of course, less control of the subjects in these studies than in the previous two, and, as the author points out, the influence on eating of non-physiological factors, e.g., social customs and meal patterns, is probably considerable. The experimental periods were short.

From these last three groups of studies it is clear that the day-to-day regulation of energy intake plays almost no part in the maintenance of body weight under the conditions of variable daily energy expenditure encountered in normal human living. The burden falls on the long-term regulation.

Lactation

A generalised picture of the changes in body weight and food consumption in rats and mice during pregnancy and lactation is given in Figure 1. It is based on the findings of Cole and Hart (1938), John and Schick (1923), Kennedy (1952-53), Mirone (1948), Morrison (1956), Murray (1941), Nelson and Evans (1948), Shukers, Macy, Donelson, Nims and Hunscher (1931), Sloanaker (1925 and 1927) and Wang (1925). The exact shape and magnitude of the food consumption curve during lactation is not certain. They vary considerably from one report to another; the broken lines indicate the magnitude of this variation.

During pregnancy animals show positive energy and water balances and an increasing body weight. There is evidence from the energy exchange experiments of Morrison (1956) that the

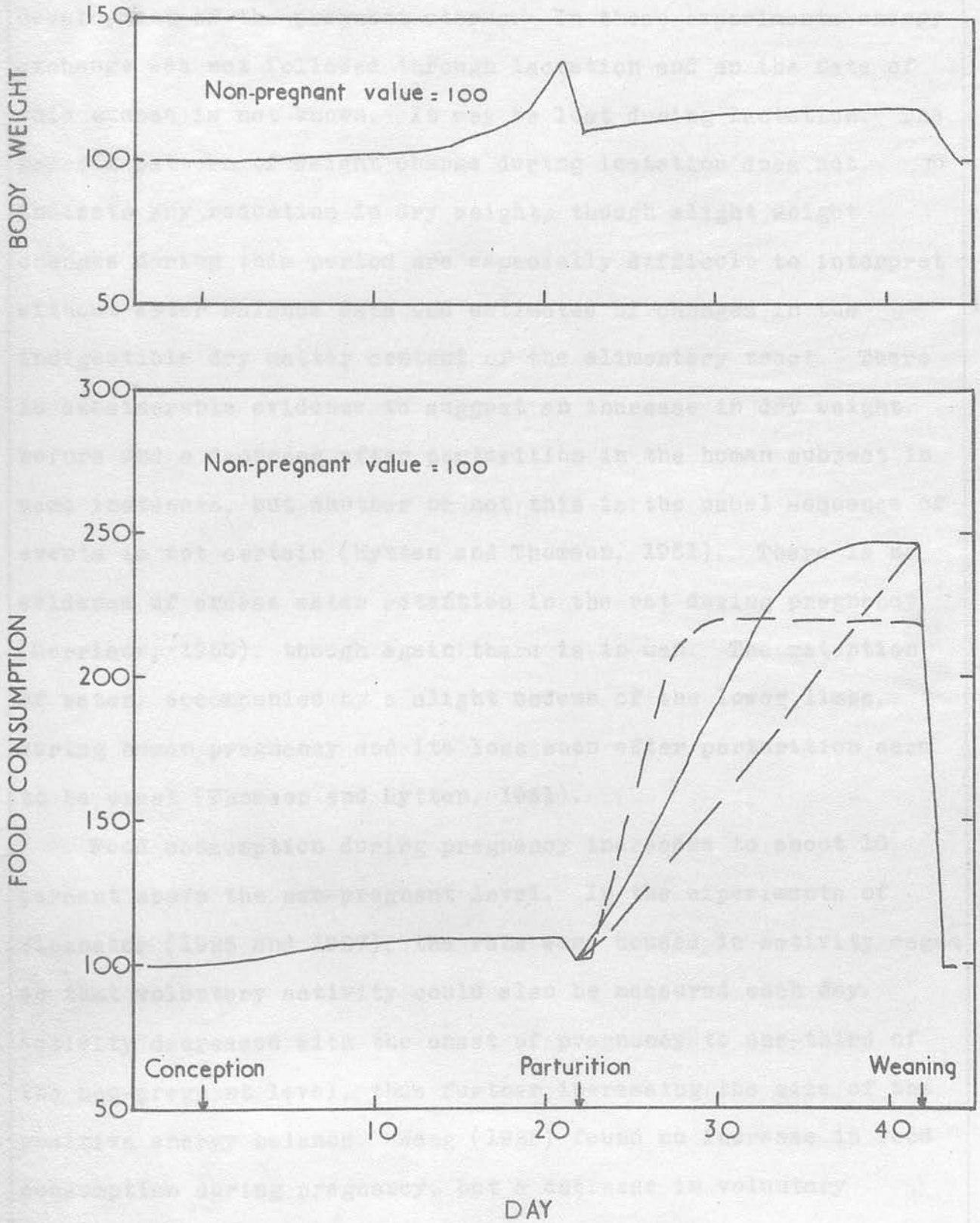
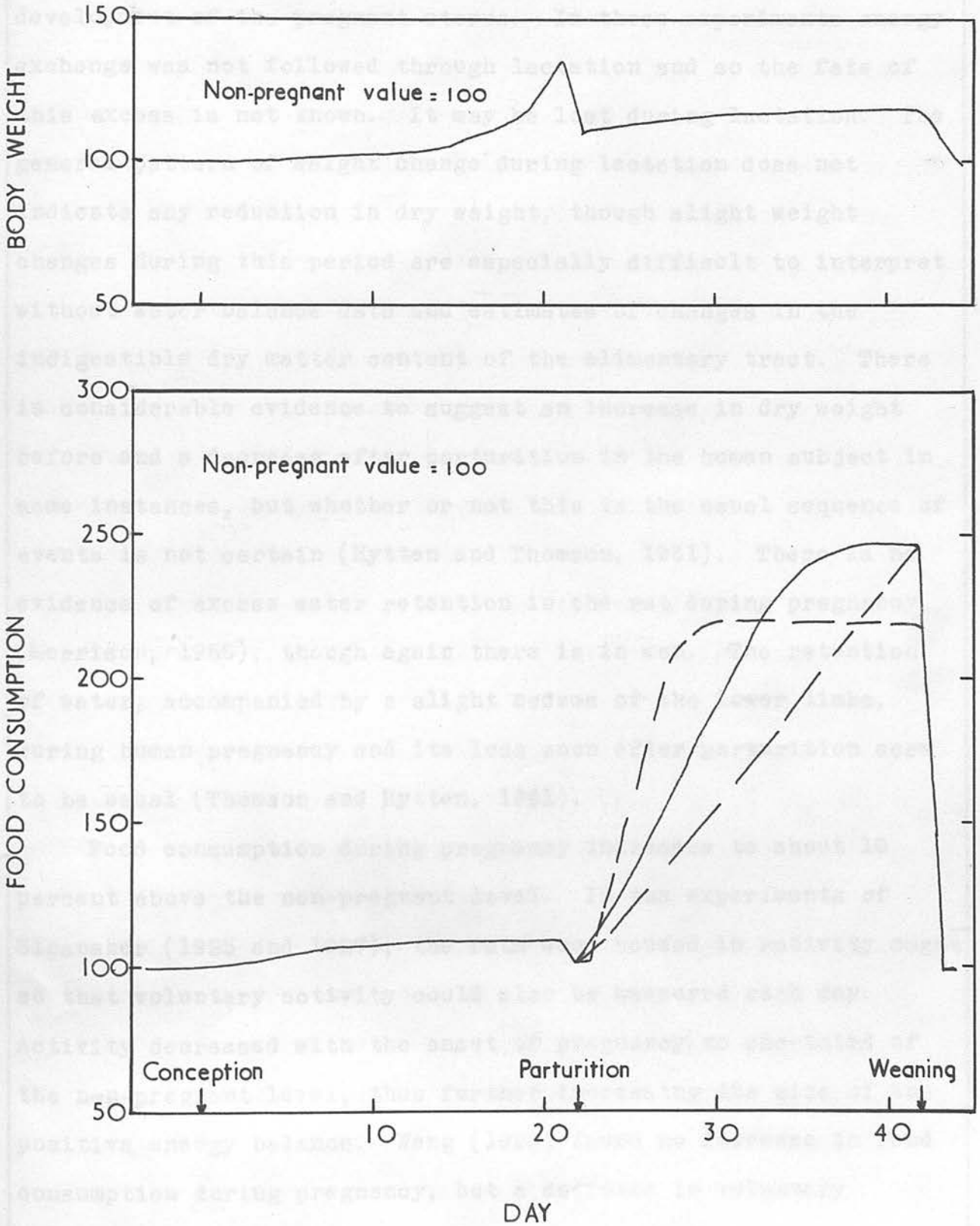


Figure 1. Changes in food consumption and body weight of a rat during pregnancy and lactation


BODY WEIGHT
150
100
50
Non-pregnant value = 100
FOOD CONSUMPTION
300
250
200
150
100
50
Non-pregnant value = 100
Conception
Parturition
Weaning
10
20
30
40
DAY

retention of energy is in excess of the amounts used for the development of the pregnant uterus. In these experiments energy exchange was not followed through lactation and so the fate of this excess is not known. It may be lost during lactation. The general pattern of weight change during lactation does not indicate any reduction in dry weight, though slight weight changes during this period are especially difficult to interpret without water balance data and estimates of changes in the indigestible dry matter content of the alimentary tract. There is considerable evidence to suggest an increase in dry weight before and a decrease after parturition in the human subject in some instances, but whether or not this is the usual sequence of events is not certain (Hytten and Thomson, 1961). There is no evidence of excess water retention in the rat during pregnancy (Morrison, 1956), though again there is in man. The retention of water, accompanied by a slight oedema of the lower limbs, during human pregnancy and its loss soon after parturition seem to be usual (Thomson and Hytten, 1961).

Food consumption during pregnancy increases to about 10 percent above the non-pregnant level. In the experiments of Sloanaker (1925 and 1927), the rats were housed in activity cages so that voluntary activity could also be measured each day. Activity decreased with the onset of pregnancy to one-third of the non-pregnant level, thus further increasing the size of the positive energy balance. Wang (1925) found no increase in food consumption during pregnancy, but a decrease in voluntary exercise of 90 percent.

With the onset of lactation, food consumption increases steadily to a peak 250 percent above the non-pregnant level in the latter half of the lactation period. In most experiments the increase in food consumption occurred gradually over the course of the lactation, paralleling the increase in body weight (and thus presumably an increase in milk consumption) of the young. The magnitude of the increase in average daily food consumption during lactation is related to the amount of milk produced, relative milk production being estimated by the number of young suckled and their rate of growth (John and Schick, 1923; Kennedy, 1952-53; Murray, 1941; Nelson and Evans, 1961; and Sloanaker, 1927). After weaning food consumption decreases quickly to the non-pregnant level.

Body weight does not return to the non-pregnant level at parturition but only after weaning, body weight during lactation being maintained, on the average, 15 percent above the non-pregnant level. Whether or not this corresponds to a different equilibrium level of dry weight is not clear. Milk and an increased alimentary indigestible dry matter content may largely account for this greater body weight.

A similar pattern of energy intake during pregnancy and lactation has been reported by Shukers et al. (1931) for three human subjects living in their own homes. During pregnancy there was a reduction in voluntary activity. At the close of pregnancy intake decreased. Average energy intake during lactation (14 month lactations) was 60 percent above the pregnant level; individual levels were ranked in the same order of

magnitude as the individual milk yields. Two of the women, those producing the most milk, lost weight during lactation and the third gained. When lactation ceased energy intake fell to the level recorded during pregnancy.

Increased basal metabolic rate

Prolonged administration of thyroxine considerably increased food consumption in white mice in an experiment by Donhoffer and Vontoyky (1947). The increase followed the rise in oxygen consumption after a lag of some days and persisted for a similar period after the fall in the rate of metabolism. Body weight decreased and stabilised at a lower level during the period of thyroxine administration. The additional calories ingested during the period of increased metabolic rate were furnished almost entirely by a starchy food, free selection of foods rich in either carbohydrate, fat or protein being allowed.

Food dilution

Adolph (1947) diluted a standard laboratory rat food with various proportions of a powdered cellulose preparation. The cellulose content of the resulting mixtures was 33, 50, 67, 75, 83 and 86 percent by weight. When these mixtures were substituted for the pure food, consumption of total solids increased on the 33, 50, 67 and 75 percent mixtures. The increases on the 33 and 50 percent mixtures were sufficiently large to maintain the previous level of food intake, but were insufficient to do so with the 67 and 75 percent ones. Total solids intake decreased markedly on the 83 and 86 percent mixtures, and consequently the intakes of food also. With the two highest and two lowest dilutions, the transition from the level of solids intake on the

pure food to that on the mixture was complete in one day, while for the intermediate dilutions, the 67 and 75 percent ones, it was gradual. On the 33 and 50 percent mixtures animals were able to maintain constant body weight, but not on those of greater dilution. Similar results were obtained when the food was diluted with kaolin. Kennedy (1950) also found a 50 percent dilution (with kaolin) to be the maximum at which constant food consumption could be maintained by young rats.

In these experiments the rats obviously demonstrated a limit to the amount of solids they could consume; and this limit was the amount consumed on the 50 percent mixtures. They did not consume more than this with the more dilute mixtures and thus their food intake decreased in rough proportion to the increase in dilution from 50 to 75 percent. Low solids intakes on the 83 and 86 percent mixtures may have been due to a reduced palatability. This factor of palatability seems to have entered more prominently into the experiments of Janowitz and Grossman (1949). They found that rats maintained food intakes and body weight at 25 percent dilution (with cellulose), but not at 35, 50 or 65 percent. But judging by the demonstrated amounts of solids the rats were capable of consuming, they could have maintained food intake and body weight on the 35 and probably even the 50 percent mixtures. The concentration of the food used (kcal./g.) was identical with that of the food used by Adolph (1947). Palatability is an important factor with older naturally obese rats. Kennedy (1950) reports that diluted food mixtures that are readily accepted by young rats are initially

rejected by older obese animals. After losing considerable weight they gradually consume enough of the mixtures to re-establish energy equilibrium and a constant (but lower) body weight. If the undiluted food is again offered at this stage, voracious eating and rapid weight gain ensues until the original body weight is restored. Intake then falls sufficiently to re-establish energy equilibrium. With the active young animal, however, initial rejection quickly results in hunger of sufficient intensity to compel acceptance, in most cases, of all but the most dilute diets.

Kennedy (1952-53) found that the critical level of dilution for lactating rats, with their higher basal level of food consumption, was lower than that for non-lactating. Lactating rats managed to maintain food intake, body weight and level of milk production at 33 percent dilution (with kaolin) but not at 50 percent.

Abgarowicz (1948) added varying quantities of sawdust to a prepared food rich in carbohydrates to obtain mixtures with a range of organic matter digestibility from 87 to 41 percent, the digestibility of the sawdust being nil. The voluntary consumption of these mixtures by rabbits was then determined. The relationship between the amount of digestible organic matter consumed in grams per animal per day (y) and the organic matter digestibility percentage (x) over this range was given by the regression equation: $y = 67.17 - (100 - x)$*. The amount of

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*(100 - x) is the indigestibility percentage. Indigestible organic matter is termed "ballast" (Lehmann, 1941). This term is the ballast percentage.

digestible organic matter consumed decreased with, but not in proportion to, the decrease in organic matter digestibility; organic matter intake increased considerably with decreasing organic matter digestibility. Similar results were obtained by Goldstein (1950) with pigs, using sawdust to vary the organic matter digestibility from 93.4 to 63.8 percent. His average regression equation was (x and y in kg.): $y = 2.235 - 0.0126 (100 - x)$. He states, however, that digestible organic matter intake decreased sharply when the organic matter digestibility fell below 71 percent. Here again, a definite limit to the amount of solids which can be consumed seems to have been reached. It is worth noting that both these investigators found, with increasing level of solids intake, an increasingly rapid rate of passage of undigested residues. Thus increasing levels of solids intake do not result in a corresponding increase in the amount of digesting solids in the alimentary tract. A concept of limiting physical capacity for solids ingestion must probably include the concept, not only of a limiting static capacity or size, but also of a limiting rate of turnover, i.e., a least time of retention of solids in the alimentary tract.

Intermittent starvation

Holeckova and Fabry (1959) adapted growing female rats to intermittent starvation by gradually increasing the length of periods of fasting between days of free access to food. These rats grew more slowly than non-starved controls. When fed every other day or three times a week, they continued to gain weight. Feeding only twice a week caused a reduction in weight; this

reduction was not progressive, however, and after an initial reduction weight remained constant. When fully adapted to the twice-weekly feeding, the animals ate on the average 112 g. of food per week in 2 daily portions, whereas the non-starved controls ate on the average 133 g. per week in 7 daily portions. Here then, is another example of an environmental stress too severe for the regulatory processes to cope with and which therefore caused a continuous reduction in the body weight (in this case the rate of increase in the body weight). The others were observed in food dilution experiments (cf. pages 40 and 41). The greatly increased quantity of food consumed in one day in this experiment led to hypertrophy of the stomach mucosa and musculature, with great increase in size. After feeding the animals normally again, this hypertrophy gradually disappeared.

The regulation of energy expenditure

While the regulation of energy intake is the chief means by which constancy of dry weight is maintained, the regulation of expenditure does occur in some circumstances. The most common is when external factors limit food consumption. Nelson and Evans (1961) found that milk yield, as judged by weaning weights of the young, decreased proportionately with the progressive reduction in the amount of food offered below the amount voluntarily consumed. Body weight decreased. Similar effects have been observed (cf. page 41) when the intake of lactating rats is reduced by diluting the food with inert bulk. The reduction of dry weight would not be expected to continue until death resulted; rather milk yield would be expected to decrease eventually to a

level which was just supported by current energy intake or cease altogether long before this; milk production ceases during fasting (Brody, 1945).

In non-lactating animals, limited food consumption causes a fall in the basal metabolic rate, and the extent of this fall is relatively greater than the accompanying reduction in body mass or surface area (Keys et al., 1950). Voluntary activity decreases with restricted intake (Keys et al., 1950).

The restriction of expenditure is thus an emergency means of maintaining dry weight; it comes into operation when a negative energy balance cannot be corrected by an increased intake. When this too is not adequate, dry weight is not maintained and death results.

There are a few reported instances in which increased intake was balanced by increased expenditure. Mayer (1955b) observed a permanent increase in energy intake by a strain of genetically obese mice when they were switched from a high-carbohydrate to a high-fat diet, but as this was accompanied by an increase in expenditure, body weight remained constant. The reason for the increased expenditure is not certain, but probably has to do with the animals' abnormal intermediary metabolism (cf. footnote, page 33); normal animals adapt to changes in the chemical composition of their food by altering intake of the food to maintain a constant energy intake, and not by altering expenditure (Cowgill, 1928; Bruce and Kennedy, 1951). Janowitz and Hollander (1955) fed dogs intra-gastrically for several months with 1.75 times the number of calories they had voluntarily consumed to maintain

control levels of body weight. The dogs showed either no gain in body weight or a gain which was much less than enough to account for the extra-calories provided, indicating that energy expenditure increased.

The physiological basis of the regulation of food consumption

Present knowledge of the physiological processes regulating food consumption has been brought together and interpreted in papers by Grossman (1958) and Brobeck (1960). According to these reviewers eating can probably be considered a reflex act requiring integrated motor activity of trigeminal, facial, glossopharyngeal, vagal and hypoglossal nerves in response to impulses from the sensory components of these as well as many other nerves. Food is the stimulus for this act; when the animal is stimulated, it first investigates the food, then prehends, chews and swallows it. The brain stem, including the nuclei and primary connections of the cranial nerves, is the level of the central nervous system involved in these reflexes.

The hypothalamus is the next higher level of control and its function is assumed, on the basis of considerable evidence, to be the quantitative regulation of energy intake in accordance with expenditure. The medial hypothalamus is believed to be responsible for the sensation of "fullness" and certain areas of the lateral portion for that of hunger. Destruction of the lateral centre causes aphagia, while lesions of the medial centre cause hyperphagia. Stimulation of the lateral centre induces eating and stimulation of the medial centre inhibits eating. It is thus postulated that the lateral centre serves to facilitate

the eating reflexes while the medial acts to inhibit the same reflexes. Thus, in theory, the interaction of these two hypothalamic centres accomplishes the quantitative regulation of food consumption.

There is some evidence, at least in primates, of a still higher centre - in the cortex - influencing eating (cf. social customs and eating, page 35).

The sensory input into the hypothalamus comes from a number of sources. First there is that from postulated receptors in the hypothalamus itself - receptors sensitive to characteristics of circulating blood such as temperature and the concentrations of intermediary metabolites. Other receptors, whose sensory input into the hypothalamus is considered to be less influential, are located in the mouth, pharynx and stomach; smelling, tasting, chewing and swallowing of food as well as the distention of the stomach by ingested food all play a part in bringing about the suppression of further eating.

The relative importance of any one of these various inputs in determining the net effect of all on eating behaviour is not the same under all conditions. In concluding his discussion of gastric distention Grossman (1955) writes: "Within certain definable limits, animals will increase the volume of food eaten to compensate for dilution of food with calorically inert substances. The effectiveness of gastric distention as an inhibitor of eating must, therefore, be subject to alteration when other factors regulating food consumption change. Here then, is an instance of dynamic equilibrium between factors regulating food

intake." From this it is probably most correct to visualise the demonstrated limit to the amount of solids an animal can consume (cf. pages 40-41) as a condition where the gastric distention input to the hypothalamus is of over-riding importance, causing the cessation of eating even when facilitatory inputs from other sources are present.

Hunger is considered to be a powerful reminder of the need to eat, but does not itself participate in the control of eating. It is impossible to define hunger when no adequate definition of sensation in general is available. Certainly "gastric hunger," associated with "hunger contractions" of the empty stomach, is a component, but not an essential one; people whose stomachs have been surgically removed continue to experience the normal sensation of hunger. Grossman considers appetite in man to be the affective state of the bodily sensation of hunger; it is a desire for food or a longing for the remembered sensation of eating.

2. The Inference

In the cow body weight is actively maintained. There are clearly upper and lower levels of body weight which are rarely exceeded even under the most unfavourable (or favourable) environments; the cow rarely starves to death and never exceeds a certain limit of obesity. The object of this study has been to ascertain by what means body weight is kept within - normally well within - these limits. It was approached from the standpoint of the inference that the cow is endowed with the same

means of achieving energy equilibrium as other mammals, i.e., by regulating both energy intake and expenditure.

The facts relevant to the consideration of this inference are those which describe the behaviour of food consumption and body weight during periods of constant environmental conditions and energy expenditure, and when expenditure increases or decreases due to changes in known variables. These facts are not very clear or extensive. All that is available is a general picture of the patterns of consumption, body weight change and milk production over a number of successive lactations under commercial dairying conditions.

The dairy cow has one lactation every 12 to 15 months, each lactation being of about 10 months duration. On a diet of grass hay under these conditions of management a constant body weight is not maintained throughout the lactation cycle (from one parturition to the next). The general pattern of weight change that is observed is presented in Figure 2. The curves in this figure are constructed from data reported by Graves, Dawson, Kopland, Watt and Van Horn (1938), Headley (1930), Legates, Murley and Waugh (1956), Makela (1956), Mather, Breidenstein, Poulton and Bonnington (1960), Nevens (1927), Reid (1961), Schulze (1955) and Sherwood and Dean (1940). At parturition body weight decreases by an amount equal to the weight of the pregnant uterus, i.e., the combined weight of the calf, amniotic fluid and placenta. From this level, it continues to decrease steadily, though at a decreasing rate, for 4 to 5 months. The loss in weight is equal to about 10 percent of body weight just after

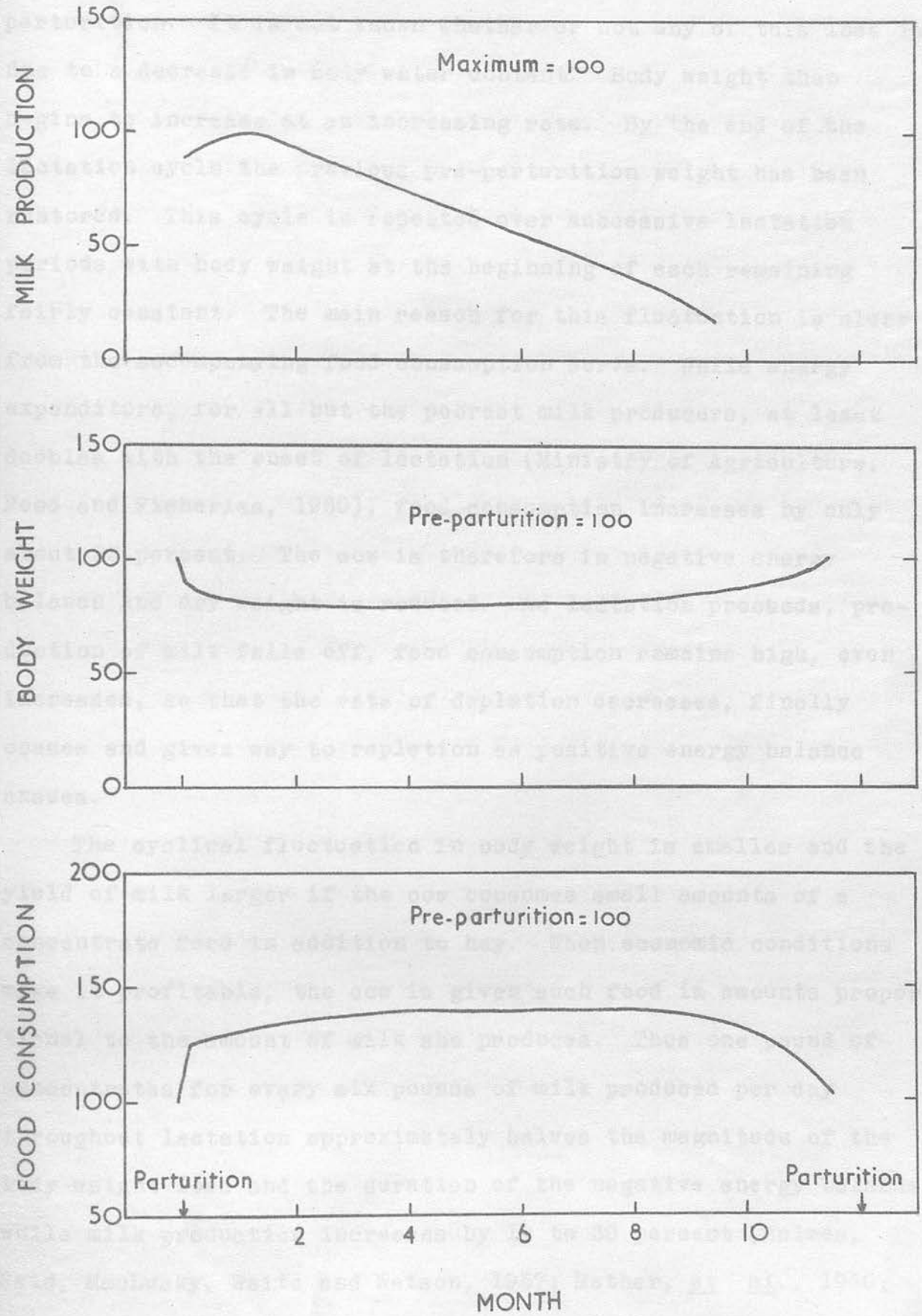
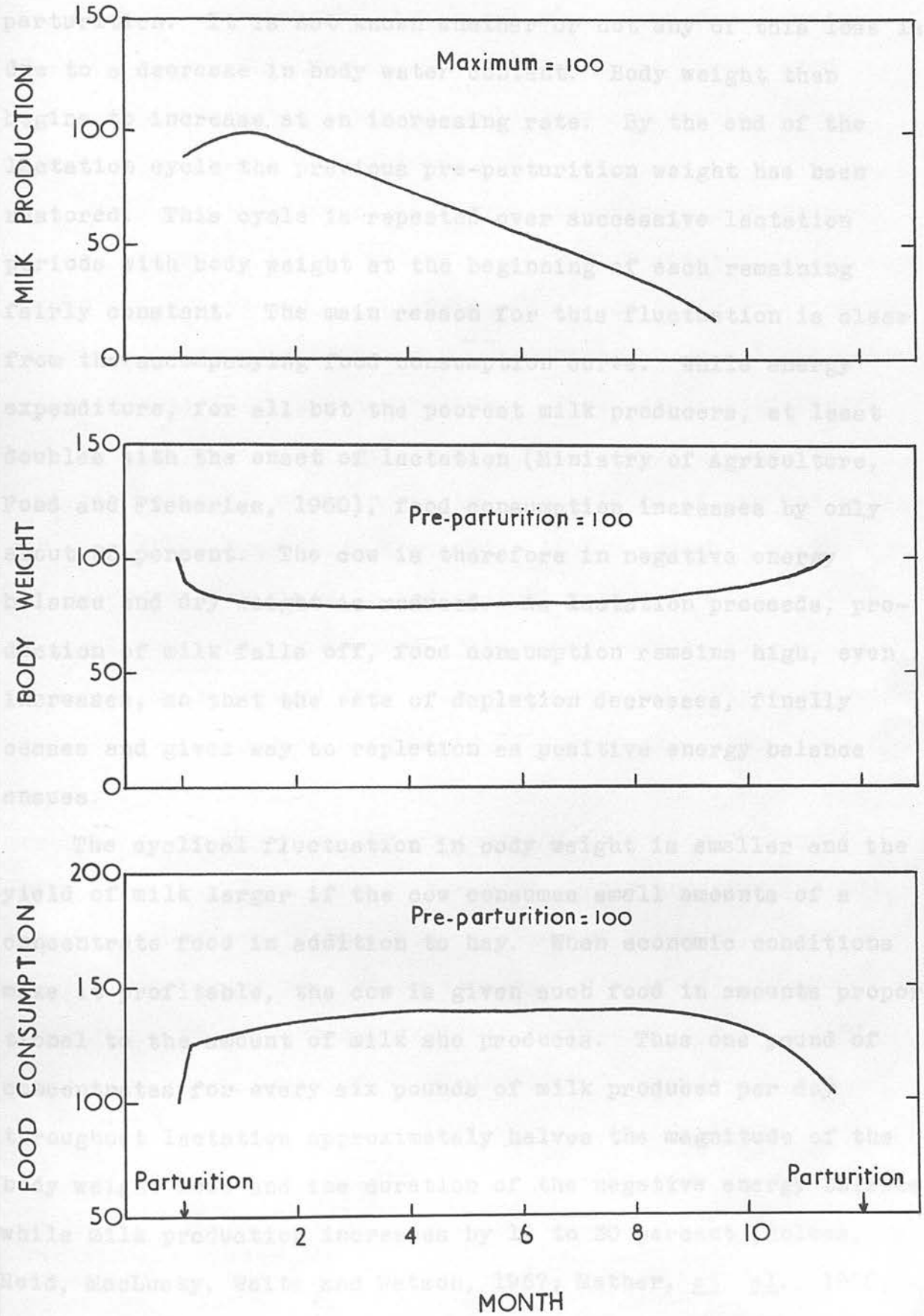


Figure 2. Changes in food consumption, body weight and milk yield for a cow during a lactation period on a hay diet.


MILK PRODUCTION
150
100
50
0
Maximum = 100
BODY WEIGHT
150
100
50
0
Pre-parturition = 100
FOOD CONSUMPTION
200
150
100
50
Pre-parturition = 100
Parturition
Parturition
2
4
6
8
10
MONTH

parturition. It is not known whether or not any of this loss is due to a decrease in body water content. Body weight then begins to increase at an increasing rate. By the end of the lactation cycle the previous pre-parturition weight has been restored. This cycle is repeated over successive lactation periods with body weight at the beginning of each remaining fairly constant. The main reason for this fluctuation is clear from the accompanying food consumption curve. While energy expenditure, for all but the poorest milk producers, at least doubles with the onset of lactation (Ministry of Agriculture, Food and Fisheries, 1960), food consumption increases by only about 25 percent. The cow is therefore in negative energy balance and dry weight is reduced. As lactation proceeds, production of milk falls off, food consumption remains high, even increases, so that the rate of depletion decreases, finally ceases and gives way to repletion as positive energy balance ensues.

The cyclical fluctuation in body weight is smaller and the yield of milk larger if the cow consumes small amounts of a concentrate food in addition to hay. When economic conditions make it profitable, the cow is given such food in amounts proportional to the amount of milk she produces. Thus one pound of concentrates for every six pounds of milk produced per day throughout lactation approximately halves the magnitude of the body weight loss and the duration of the negative energy balance, while milk production increases by 10 to 30 percent (Holmes, Reid, MacLusky, Waite and Watson, 1957; Mather, et al., 1960; Reid, 1956; and Reid and Holmes, 1956). The reason for these

effects is that total dry matter and digestible dry matter intakes increase with the consumption of concentrates; for every pound of concentrates consumed, voluntary consumption of hay decreases by only 0.2 to 0.7 pound.*

In somewhat different ways from the above experimenters, Putnam and Loosli (1959) and Nevens (1927) demonstrated the same effect of concentrates. The former prepared diets in which hay and silage made up 40, 60 and 80 percent of the total dry matter, a concentrate mixture the remainder. These diets were fed to cows ad libitum during the 8th to the 23rd week of their lactation period. With increasing proportions of hay and silage, dry matter and digestible dry matter intake and milk production all decreased. Changes in body weight were not referred to. In the experiments of Nevens (1927) two cows were allowed to select their own diets freely from a number of individual foods, including hays, cereal grains and oilseed cakes. With the onset of lactation, net energy intake increased by about 100 percent, consumption of the concentrate foods increasing relatively more than that of the hays. This increase was not, however, immediate; a peak was reached one month after parturition. From this peak, intake decreased slowly with advancing lactation. There were considerable decreases in body weight during the first month after parturition.

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*The exact replacement value is related to the dry-matter digestibility of the particular hay; the higher the digestibility, the larger the replacement value, i.e., the greater the amount of it replaced by a pound of concentrates (Blaxter, Wainman and Wilson, 1961).
Another important reason for these effects of concentrates is, of course, that the net energy content of concentrate dry matter is greater than that of hay dry matter.

These patterns of food consumption, body-weight change and milk production, and their variations on different diets, indicate that the cow consuming an all-hay diet maintains constancy of dry weight primarily by regulating energy expenditure. With the onset of lactation potential energy expenditure (in the form of milk) increases; but as energy intake does not increase proportionately, actual expenditure is restricted to a level considerably below this potential. The actual level is that at which the cow maintains the same average dry weight from one lactation period to the next. Within periods, of course, dry weight fluctuates widely and regularly around the average. This average dry weight may be the minimum compatable with long term health.

This behaviour is very different from that of the lactating rat on a normal diet. It is, however, similar to what would be expected of the rat if handicapped by an external factor which lowered the level to which food intake could be raised in response to the increased energy expenditure of lactation. Such a factor is the dilution of the normal diet with nutritionally inert bulk (cf. page 41). She would probably demonstrate progressively increasing levels of milk production and stability of body weight as the bulkiness of her diet decreased to a critical level. In other words, she would move gradually from a situation in which body weight was maintained (rather poorly) by the regulation of energy expenditure to one in which it was maintained by the regulation of energy intake. With the cow the analogous dietary factor appears to be the great natural bulkiness of hay diets and those of similar foods.

Definition of bulkiness

The validity of the preceding analogy rests on the definition of the term "bulkiness". This is best done with reference to the limit of physical capacity for food ingestion (cf. page 42). With consumption at the limit of this physical capacity, the digestible dry matter intake will vary from food to food.* The lower this intake the more bulky the food. Therefore, there is a critical level of bulkiness above which a given energy intake by a given animal cannot be maintained.

Two factors determine the bulkiness of a food. First is the digestibility of its dry matter.** The lower the dry-matter digestibility coefficient, the bulkier is the food. Diluted rat food is bulkier than the pure food because the added cellulose and kaolin are indigestible. Hay is bulkier than concentrates because its digestible dry matter content is usually lower.

Second is the rate at which dry matter is digested.*** This determines how long on the average ingested dry matter remains in the alimentary tract. The longer dry matter remains in the alimentary tract, the greater the alimentary content of digesting dry matter, the less the physical capacity available at any

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*This is a theoretical statement as most foods are never consumed at this level.

**The water contained in food is disregarded as it appears to have little or no influence on consumption (cf. the discussion by Makela, 1956, pp. 43-45).

***The rate of digestion is defined here as the rate at which ingested dry matter is reduced to physical and chemical proportions which enable it to leave the alimentary tract.

subsequent time for further dry-matter ingestion, the lower the dry-matter and digestible dry-matter intake, the bulkier is the food. The diluted rat food is probably digested at the same rate as the undiluted, the food dry matter being common to both. With cow foods, however, the rate of digestion varies considerably.

The relationships among dry-matter digestibility, rate of dry-matter digestion, dry-matter and digestible dry-matter intake were demonstrated by Blaxter et al. (1961) for a group of hays. The dry-matter and digestible dry-matter intake increased rapidly as digestibility increased from 38 to 70 percent and thereafter more slowly. The rate of passage of undigested residues (as an index of the rate of dry matter digestion) also increased, so that the dry-matter content of the alimentary tract was the same for all hays after the daily meal. A direct relationship between the digestibility in vitro and the rate of digestion of dry matter was also found by Crampton, Donefer and Lloyd (1960).

Campling, Freer and Balch (1961) found the consumption of hay by fistulated cows to be more than twice that of oat straw. The dry-matter digestibilities of the hay and straw were 67.4 and 45.8, respectively. The rate of loss in weight of cotton thread suspended in the reticulo-rumen was six times faster with the hay diet. Between meals the rates of loss of food dry matter from the reticulo-rumen were 0.64 and 0.32 lb./h. for the hay and straw diets respectively, while during meals they were 1.33 and 0.51. The average retention time of indigestible dry matter in the alimentary tract was 30 percent greater (100 vs. 73 hr.) with the straw diet than with the hay. This difference

in retention times appeared to be due almost entirely to differing retention times in the reticulo-rumen, as the retention times of hay and straw particles introduced directly into the abomasum were 23 and 27 hr. respectively.* When hay consumption was restricted to the level at which straw was voluntarily consumed the rate of digestion of cotton threads was unaltered and the retention time of undigested residues in the alimentary tract was still greater for the straw (100 vs. 83 h.), thus indicating that the rate of digestion and not intake was the independent variable. In another series of experiments (Campling, Freer and Balch, 1962) the infusion of 75 or 150 g. of urea directly into the reticulo-rumen of fistulated cows on a straw diet increased voluntary consumption by 40 percent. The dry-matter digestibility was increased from 41 to 49 percent, the rate of digestion of cotton threads increased seven-fold and the mean retention time of undigested residues decreased by 27 h. (from 99 to 72 h.). Again, the magnitude of these effects was as great or nearly as great when straw intake was held constant, during the infusion of urea, at the level voluntarily consumed without the urea. The fact that the urea was infused directly into the rumen rules out palatability as a factor responsible for the increase in consumption.

Hoflund, Quinn and Clark (1948) and Donefer, Crampton and Lloyd (1960) found the voluntary consumption of hays by sheep

*There is considerable evidence in addition to this that the reticulo-rumen is the critical region of the alimentary tract with respect to the limitation of food intake (Balch, 1950; Blaxter, Graham and Wainman, 1956; Blaxter et al. 1961; Campling and Balch, 1961; Meyer, Gaskill, Stoewsand and Weir, 1959; Stallcup, Cason and Walker, 1956).

to be directly related to the rate of cellulose digestion *in vivo*. In view of the findings of Campling *et al.* (1961) this relationship can be considered a casual one.

The consumption of a given hay is usually increased by grinding and pelleting it (Beaty, McCreery and Brooks, 1960; Cullison, 1961; Keith, Hardison, Huber and Graf, 1961; Klosterman, Ricketts and Johnson, 1960; Lloyd, Jeffers, Donefer and Crampton, 1961; Meyer *et al.*, 1959; Wallace and Hubbert, 1959; Wallace, Raleigh and Sawyer, 1961; Webb, Cmarik and Cate, 1957). The digestibility of dry matter is usually not altered, though that of the fibre is sometimes reduced. Keith *et al.* (1961) found a faster rate of passage of undigested residues through the alimentary tract with pelleted material. Meyer *et al.* (1959) found that ingested dry-matter was digested more quickly in the reticulo-rumen and passed out of this compartment more quickly with the pelleted diet. Blaxter *et al.* (1956) found that ground, pelleted hay passed through the alimentary tract more quickly than the same hay in the usual form even when intake was restricted to levels below the voluntary level of intake, thus indicating that the rate of passage and not intake is the independent factor.

Concentrates are less bulky than hay because their dry matter is more rapidly digested; the rate of passage is faster, at least when they are consumed along with hay (Balch, 1950; Paloheimo and Makela, 1959), and a greater proportion of the total digested dry matter of concentrates is lost in the reticulo-rumen (Balch, 1957; Rogerson, 1958). Emery, Smith and Lewis (1958) found that the dry matter content of the reticulo-rumen

at any given time after eating decreased as the proportion of concentrates in the diet increased when total dry-matter intake was held constant. Balch, Balch, Bartlett, Bartrum, Johnson, Rowland and Turner (1955) found a reduction of approximately 25 percent in the dry-matter content of the reticulo-rumens of two cows when their diet was changed from 18 lb. hay and 10 lb. concentrates to 2 lb. hay and 24 lb. concentrates.

Bulkiness, as here defined, could thus explain adequately both the decrease in dry-matter and digestible dry-matter intake by the cow with increasing proportions of hay in her diet, and the decrease in food intake by the rat, rabbit and pig with increasing dilution of its diet beyond a critical level.

The inference was considered reasonably successful and the following hypothesis thus justified.

3. The Hypothesis

The cow is endowed with the same means of maintaining constancy of body weight as other mammals, namely, the ability to regulate both energy intake (food consumption) and energy expenditure. Under modern dairying conditions, however, she relies more on the latter than on the former. The extent to which food consumption can increase in response to increased energy expenditure (in the form of milk) is severely limited by the bulkiness of diets composed of hay and similar foods. Milk production is therefore limited to a level at which minimum level of dry weight can be maintained.

Testing of Hypothesis

1. Experimental Method

It has been postulated that the regulation of energy intake is a possibility with the cow, but that it plays an insignificant part in the maintenance of dry weight on an all-hay diet under a commercial dairying regime due to the great bulkiness of the hay. Its relative importance would, therefore, be greater, probably predominant, on a less bulky diet. The experimental approach to testing this hypothesis has accordingly been to offer cows a diet of low bulkiness and to observe their patterns of food consumption and body-weight change under conditions of low and constant energy expenditure (maintenance) and of variable energy expenditure (maintenance, pregnancy and lactation). The diet consisted of a single concentrate mixture as the sole food.

Two experiments were conducted. In Experiment 1, two dry, barren females, X and Y, were kept under uniform management on the all-concentrate diet for 13 months, from September 1961 to October 1962. Daily food consumption and body weight were determined. During the fourth month, they were given walking exercise daily.

In Experiment 2, two pairs of identical twin cows, AH and AC, BH and BC, were kept under uniform management during the last 2-3 months of pregnancy, a 5-month lactation and a 2- to 5-month post-lactation period, in all about 13 months extending over the same period as Experiment 1. One cow of each pair was given an all-hay diet (H), the other the all-concentrate diet (C). Food

consumption, body weight and milk yield were determined daily. The dry-matter digestibility coefficients of the diets and the rates of passage of their undigested residues were determined with each cow before, during and after lactation. A preliminary uniformity trial was conducted with one pair of twins (AH and AC), using an all-hay diet. Daily food consumption only was determined in this trial.

Foods

The chemical composition of the foods used and the digestibility of their dry matter are given in Table 1. Dry matter content was determined by oven drying at 100 degrees to constant weight. Further chemical analysis was performed on material ground to pass through a sieve with 1 mm. circular openings. The methods of determining ash, nitrogen, fibre, oil, and phosphorus were essentially those given in the Eighth Schedule of "The Fertilisers and Feeding Stuffs Regulations, 1960." Calcium was precipitated as calcium oxalate and determined volumetrically with potassium permanganate. The determination of dry-matter digestibility is described in a separate section (page 73).

Table 1. Chemical composition and dry-matter digestibility of the experimental foods

Food	Dry Matter (%)	Ash	CP	Fibre	Oil	Ca	P	DM Digest (%)
		(as a percentage of the dry matter)						
Hay no.1	--	6.4	11.3	28.5	0.9	0.50	0.41	--
Hay no.2	83.2 ± 0.51	8.7	13.1	30.6	1.1	0.72	0.50	64.1 (4)*
Hay no.3	82.6	6.8	15.0	27.9	1.0	0.49	0.40	66.5 (2)*
Concentrate mixture	86.3 ± 0.14	4.4	16.9	6.2	3.5	0.48	0.53	74.5 (6)*

*The number of individual determinations averaged

All the hays were made from well-fertilised and managed perennial rye-grass swards. The grass was cut at or slightly before ear emergence.

Hay no.1 was used in the uniformity trial with cows AH and AC. It was made from the second cutting of grass in the season, partially dried in the field, baled and then further dried in a stack with forced cold air. A composite sample of all the material offered to the cows was obtained by mixing together a large number of handfuls taken during the course of the trial. The dry matter percentage and dry matter digestibility were not determined.

Hay no.2 was fed to cows AH and BH throughout Experiment 2, except for the last six weeks. It was made from third-cutting grass, well cured in the field on tripods. Colour and smell were good. Due to improper baling of some of the material and problems of storage, the total amount of hay actually available for feeding was less than intended and was insufficient for the entire experiment. Bales from different parts of the field were completely mixed in several handlings. A sample of the hay was obtained when it was brought from the field and analysed for calcium, phosphorus and nitrogen. From calcium and phosphorus contents minimum daily intakes of these two minerals were estimated. These estimates were well above those recommended by the (U.S.A.) National Research Council (Morrison, 1955). The crude protein content (nitrogen content x 6.25) indicated that the hay was similar in quality to the hay ("Ryegrass, perenial") listed in "Rations for Livestock" (Bulletin No.48,

Ministry of Agriculture, Fisheries and Food, 1960) which has a digestible crude protein content of 7.4, and a starch equivalent value of 45 (both on a dry matter basis) and a D.C.P.:S.E. ratio of 1 to 6. During the course of Experiment 2 samples of the hay offered to the cows on 7 randomly chosen days were obtained. They were dried, milled and stored in waxed cartons. A bulk sample was later prepared from these individual samples, material from each being contributed in proportion to the dry matter content of the original sample. The complete chemical analysis was performed on material from this bulk sample.

Hay no.3 was made from second-cutting grass. It was badly discoloured and had a sweet smell. A sample was obtained by mixing a large number of handfuls of the hay obtained from the stacked bales. The bales were handled several times before being used and were probably well mixed. This hay was fed to cows AH and BH for 6 weeks at the end of Experiment 2.

The material composition of the concentrate mixture was as follows:

96 lb.	Groundnut Meal (decorticated)
160 lb.	Maize Meal
160 lb.	Barley Meal
384 lb.	Bruised Oats
5 lb.	Ground Limestone
10 lb.	Sodium Bicarbonate
5 lb.	Vitamin A and D Supplement (Containing 8 million IU of vitamin A and 2 million IU of vitamin D_3)
820 lb.	

Factors from standard food composition tables ("Rations for Livestock," Bulletin No.25, Ministry of Agriculture, Fisheries and Food, 1960) were used to calculate the digestible

crude protein and starch equivalent contents of this mixture. They were, respectively, 13.7 and 76 (on a dry matter basis). The D.C.P.:S.E. ratio was 1 to 5.6, close to that estimated for hay no.2. It was thought necessary to keep these ratios similar in Experiment 2 in order to avoid any possible effects of differing proportions of protein. According to recommended allowances, an average dietary D.C.P.:S.E. ratio of 1 to 6 is adequate for lactating cows producing up to 5 gallons of average milk per day. A preliminary mixture of the basic ingredients (i.e., the groundnut meal, maize, barley and oats) was analysed for calcium and phosporus. The phosphorus content was found adequate, the content of calcium inadequate. The rate of limestone supplementation was adequate to insure daily calcium intake by all cows equal to those recommended by the (U.S.A.) National Research Council (given in Morrison, 1956). The vitamin A and D supplementation was adequate to insure the daily intakes recommended for the lactating cows by the National Research Council (given in Maynard and Loosli, 1956). The rate of sodium bicarbonate addition was somewhat arbitrarily chosen; at 1.2 percent of the ration, it fell between the 2.5 percent used by Preston, Whitelaw, MacDearmid, MacLeod and Charleston (1961) for fattening calves and a figure of 0.8 percent suggested by Armstrong (1961). The mixture was made up every 7 to 10 days as required in 820-lb. batches. The sample of this mixture used for chemical analysis was obtained in the same way as that of Hay no.2.

Apart from their food, each animal was given approximately 10 g. of a mineral mixture of the following composition,

21.6	kg.	Sodium Chloride
1.2	kg.	Ferrous Sulphate
605	g.	Manganese Carbonate
9.6	g.	Potassium Iodide
19.2	g.	Cobalt Sulphate
96	g.	Copper Sulphate

The mixture was based on that suggested by Purves and McDonald (1961). The cows also had plain salt to appetite. Water was continuously available in individual drinking bowls.

Cows

It was not possible to accommodate more than two pairs of cows on Experiment 2. The highest degree of uniformity within the two pairs for a large number of traits, not all of which were even specified at the outset of the experiment, was therefore essential and was thought to be assured with monozygous twins.

The life histories of AH and AC, BH and BC are given in Table 2. These animals were purchased from the Animal Breeding Research Organisation for use in this study. Each pair had been managed as a unit throughout its life in connection with genetic investigations. Each cow within pairs was randomly assigned her letter on arrival at the University farm. Both pairs were Ayrshire-Shorthorn cross, but in AH and AC the Ayrshire was predominate, in BH and BC the Shorthorn, AH and AC possessed considerable dairy character, BH and BC very little. AH and AC were quick and bright, BH and BC sluggish and dull. Nevertheless, AH and AC were less easily disturbed or frightened. Both pairs handled easily. AH and AC calved 9 days apart during the experiment, BH and BC 15. None of them was rebred during the course of the experiment.

Cows X and Y had been discarded from the commercial milking herd because they failed to conceive. X was 9 years old at the start of the experiment and had completed 5 lactations; Y was 13 years old and had completed 8 lactations. Their milk production records were similar and just average. Their failure to conceive was probably connected with an abnormal hormonal balance. Such an abnormality was suggested by the development, particularly in X, of male secondary sexual characteristics (thickened neck and bull-like roaring and pawing the ground) and intermittant periods of nymphomania. Both were of a nervous and wary temperament and would not eat in the presence of a person. X was defiant and often sullen, Y meek and martyred. These differences in their personalities were most clearly demonstrated in their reaction to the forced exercise.

Table 2. Life histories of experimental animals AH, AC, BH and BC*

Cow	Age at parturition (years and days)			Weight following parturition (lb.)			Lactation milk yield (lb.)**			Age when purchased (years and days)
	1st	2nd	34d	1st	2nd	3rd	1st	2nd	3rd	
AH	2-117	3-120	4-110	862	940	1010	4543	5952	6386	5-10
AC	2- 81	3- 94	4-120	862	940	1010	3929	5747	6067	5-10
BH	2- 78	3-120	-	952	1180	-	4372	6101	-	4-50
BC	2- 83	3-103	-	962	1130	-	3893	5596	-	4-50

*This information was supplied by the Animal Breeding Research Organisation, Glenbourne, South Oswald Road, Edinburgh 9.

**These figures are the 4 percent fat-corrected totals for the first 150 days of the lactation. The over-all average butterfat content of the milk produced was 3.8 and 4.0 percent for pairs AH and AC, BH and BC respectively.

Determination of food consumption

Food consumption was determined on a daily basis. Food in excess of what an animal would consume during a 24-hr. period was weighed out one morning and the leavings were weighed the following morning. The food consumed was taken as the difference between the amount offered and the amount left. The spilling and stealing of food were prevented (cf. section on housing and management, page 69).

To ensure that no subjective bias entered into the determination of voluntary consumption, the amount of food offered was determined by a constant formula. The formula was essentially that of Blaxter, Wainman and Wilson (1961). On any day that the amount of food refused was less than 10 percent of that offered, the following day's offering was increased to 110 percent of the amount consumed on that day. If the amount refused was more than 10 percent of that offered, the following day's offering was the same, unless the smallest refusal on any day during the preceding 7 days was greater than 10 percent of the amount offered; in this case the following day's offering was 110 percent of the amount consumed on that day. The primary function of the formula was to ensure that the animal was always offered more than it would consume; hence the rapid upward and cautious downward adjustment of the amount of food offered. Its second function was to maintain a more-or-less constant proportion of leavings; this was desirable because the material composition of the food remaining in the feeding box changes as the animal proceeds with her eating - the proportion of fine particles

increases. The value of 10 percent, though lower than that used by Blaxter et al. (1961) (for the sake of economy in foods), allowed the formula to serve these two functions satisfactorily. There were very few days when an animal ate all of the food offered her. These instances occurred mostly with X and Y whose daily consumption was more variable than that of the others.

All weighings of food were done on a platform balance which weighed to the nearest quarter pound. With two weighings to determine each day's consumption, the maximum weighing error to which a single value was liable was ±0.25 lb. roughly 1 percent of the amount determined.

Determination of changes in dry weight

Changes with time in average body weight were considered to represent quantitative changes in dry weight. Though the absolute variation in daily weights is large, and occasional changes in weight from one day to the next are amazingly large (e.g., 50 lb.), the relative variation is only 25 percent larger than that encountered in man under similar circumstances, as will be seen from Table 3. The coefficients of variation for the men subjects were calculated from individual weights given by Durnin (1961). The six men were under closely controlled environmental conditions (military training) and were weighed on six consecutive days on arising from bed, naked and after emptying the urinary bladder. The coefficients of variation for the bovine subjects were calculated from individual weights obtained in the present experiments. For each cow three groups of six consecutive daily weights were chosen at random during

Table 3. The variation in daily body weight of men and cows

Subject	Day 1	2	3	4	5	6	Mean	Coeff. of Variation (%)
(Human)* (Weight in Kg.)								
A	78.3	78.2	77.4	78.2	78.4	77.1	77.9	0.69
J	66.0	66.2	66.7	67.0	67.1	66.1	66.6	0.68
P	86.7	87.2	88.3	88.1	88.0	87.9	87.7	0.71
S	64.4	65.0	64.8	65.0	64.3	64.1	64.6	0.60
T	65.1	66.4	65.7	65.9	65.1	65.1	65.6	0.82
W	69.4	69.5	69.3	69.6	69.4	69.0	69.4	0.32
							Human mean	0.64
(Bovine) (Weight in lb.)								
AH	1267	1263	1265	1269	1280	1276	1270	0.52
	1002	986	982	1000	992	1002	994	0.87
	994	986	992	1006	991	984	992	0.79
							Mean	0.73
AC	1106	1116	1114	1104	1102	1092	1106	0.79
	1112	1106	1106	1110	1098	1091	1104	0.72
	1092	1088	1100	1084	1074	1084	1087	0.80
							Mean	0.77
BH	1294	1310	1320	1330	1311	1318	1314	0.92
	1037	1038	1032	1044	1038	1056	1041	0.80
	1056	1050	1060	1046	1065	1062	1057	0.69
							Mean	0.80
BC	1137	1158	1145	1142	1132	1132	1141	0.86
	1134	1126	1126	1148	1127	1156	1136	1.13
	1170	1178	1184	1164	1165	1158	1170	0.82
							Mean	0.94
X	1492	1498	1949	1496	1507	1499	1498	0.35
	1448	1437	1419	1443	1435	1463	1441	1.02
	1440	1436	1414	1417	1408	1448	1427	1.14
							Mean	0.84
Y	1268	1266	1261	1245	1242	1252	1256	0.87
	1242	1230	1228	1226	1234	1242	1234	0.57
	1085	1087	1076	1070	1066	1080	1077	0.77
							Mean	0.74
							Bovine mean	0.80

*Data from Durnin (1961). Elkington and Danowski (1955 report a coefficient of variation for the mean daily body weight of a single man over a period of 53 consecutive days of 0.51.

periods when weight was not increasing or decreasing.

During pregnancy and early lactation, change in body weight may not be as reliable an index of change in dry weight as it is at other times. The reasons for this have been mentioned with reference to rats and men (page 37). There were no indications in these experiments of excess water retention during pregnancy. An increase in the amount of indigestible dry matter in the alimentary tract after parturition was indicated for AH and BH and an attempt was made to estimate its magnitude (cf. page 78).

Weighings were done on a large platform balance which weighed to the nearest 2 pounds. It was necessary to determine a tare daily and subtract it from the values read from the scale. The maximum weighing error of a single body weight value was, therefore, ±2 lb., not more than 0.2 percent of the value determined.

Housing and management

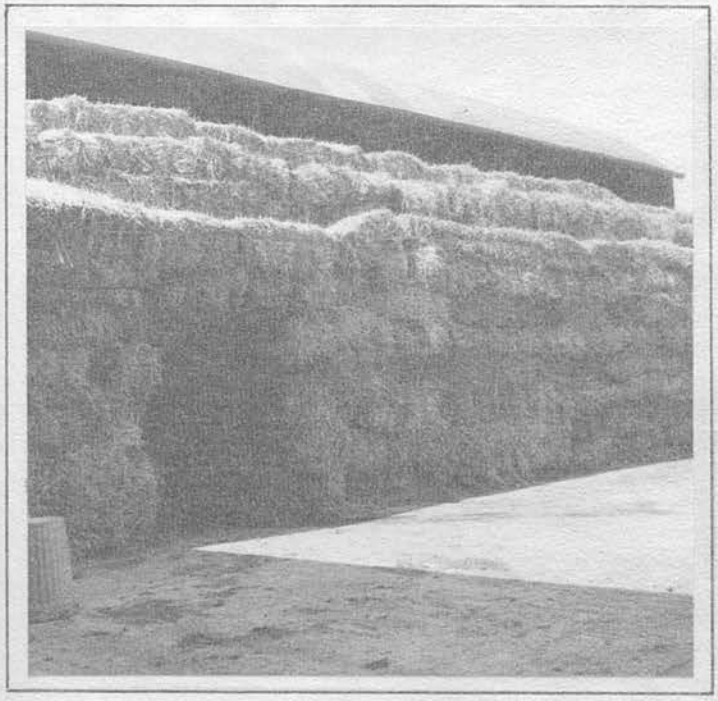
The animals were housed in an ordinary corrugated-iron farm shed that is normally open along one side. During the experiments this open side was closed with a wall constructed of straw bales. It was, however, still draughty and only a few degrees warmer than the out-of-doors. The mean monthly minimum and maximum temperatures (Fahrenheit) inside the shed for the period of the

experiment were:

Month	Min.	Max.	Month	Min.	Max.
Oct.	48.8	61.6	April	37.8	64.9
Nov.	38.2	51.7	May	41.4	58.2
Dec.	30.3	44.6	June	48.7	67.2
Jan.	30.6	45.0	July	49.3	67.3
Feb.	36.5	47.4	Aug.	49.9	54.6
Mar.	30.7	45.4	Sept.	47.5	60.9

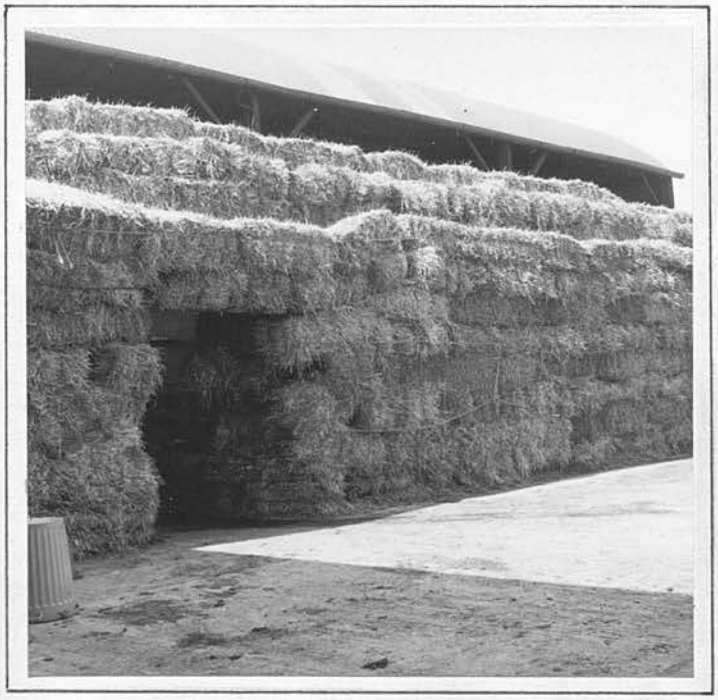
During the coldest weather water in the pipes supplying the shed frequently froze. When this happened water was carried to the animals in buckets. An effort was made to maintain the normal pattern of water consumption throughout the day during these periods, as any serious disturbance of this pattern appeared to cause unusually large changes in daily body weight.

The animals were tied in standings of wood construction (Photographs 2 and 3). Cows on the hay diet were bedded on sawdust, those on the concentrate diet, because they ate sawdust, were provided with individual foam rubber mattresses. Feeding boxes were 30 inches square (30" x 42" for hay), 48 inches high and constructed of $\frac{7}{8}$th-inch tongue-and-groove lumber (Photographs 2 and 3). They were raised 6 inches off the floor and permanently attached to the fronts of the stalls. The cows had access to the food in their boxes through key-hole shaped openings. The enlarged portions were just large enough to admit their heads and the narrow portions just wide enough to allow their necks to slide up and down. The hay-feeding boxes had curtains, supported on strong springs, covering most of the narrow portions. This design entirely prevented the spilling of food, except by cow BH, which, in spite of the difficulty of doing so, did often remove her head from the box whilst chewing



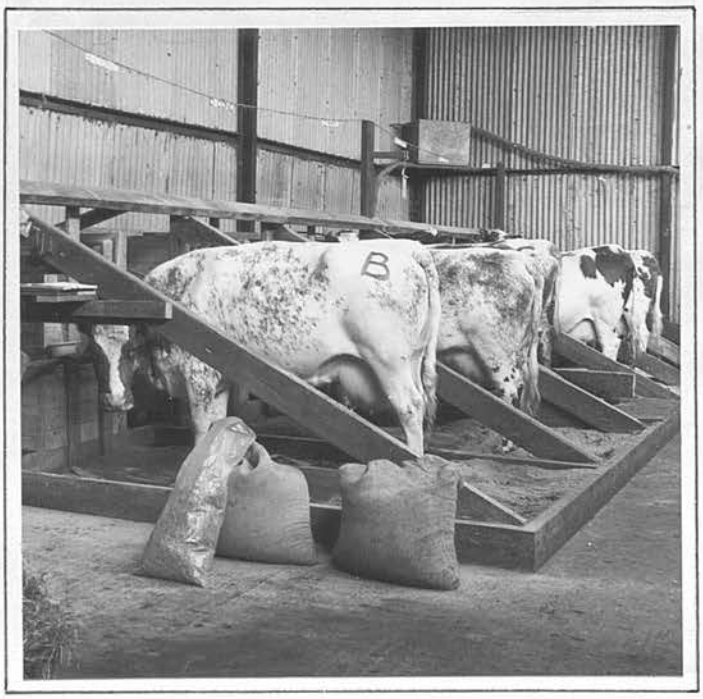
Photograph 1. A front view of the experimental shed.

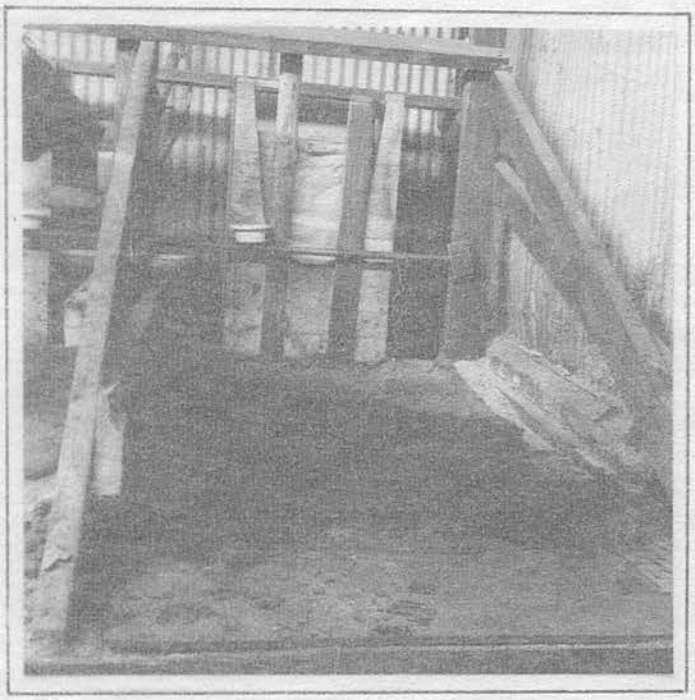
Photograph 2. A general view inside the experimental shed.



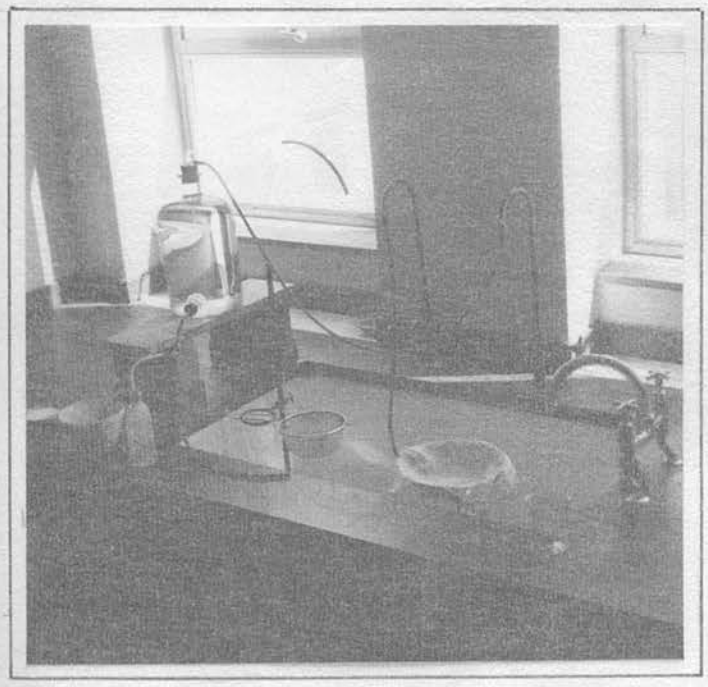
Photograph 1. A front view of the experimental shed.

Photograph 2. A general view inside the experimental shed.



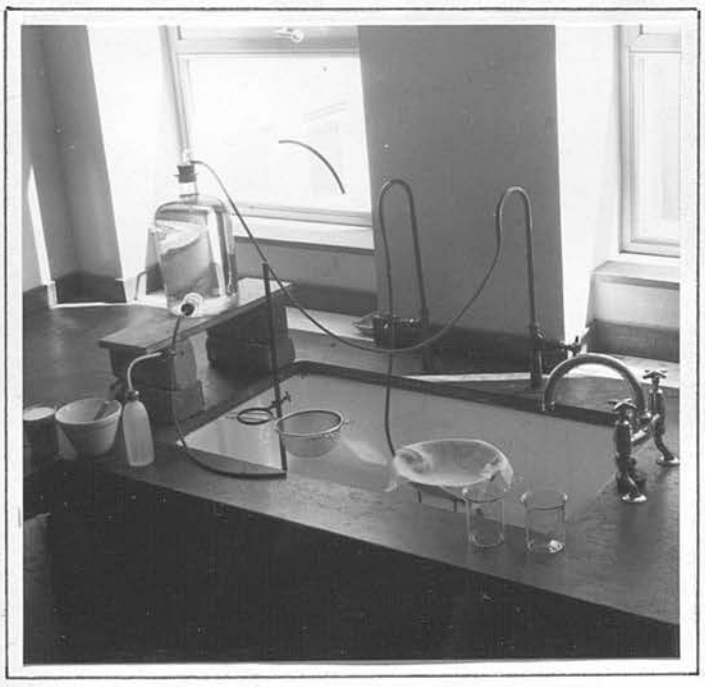


Photograph 3. A close-up view of an individual standing. The plywood sheet for collecting faeces is in place.



Photograph 4. A view of the apparatus used to prepare faeces samples for particle counting.

Photograph 3. A close-up view of an individual standing. The plywood sheet for collecting faeces is in place.



Photograph 4. A view of the apparatus used to prepare faeces samples for particle counting.

and thus dribble hay on the floor. The spilled hay was almost completely recovered, however, and added to the refusals; the amount never exceeded about one pound. The boxes were swept out by reaching in through the front opening and were filled from a catwalk at the rear.

Each cow had a constant-level watering bowl and a small polyethylene basin for salt.

Cows X and Y, and also AH and AC, BH and BC when not milking, were taken from their stalls to the weighing room at 8:00 AM. At 9:00 AM they were weighed and returned. Feeding boxes were swept out and refilled and stalls cleaned in the interval. When milking, AH, AC, BH and BC were taken to the byre at 4:00 AM and milked between 5:30 and 6:00. They were then removed to the weighing room where they remained until being weighed at 9:00. They were taken from their stalls again at 2:30 PM for the afternoon milking and returned at 4:00. The experimental "day" began at 9:00 AM one day and ended at 9:00 AM the following day. The "day's" body weight was the value determined at the end of the "day" and its milk yield was the sum of the afternoon and morning yields, i.e., the yields of those milkings falling within the "day".

Milking was done by machine. Milk was weighed at every milking to the nearest half pound on a spring scales. The cows were dried off slowly by intermittant milking at the end of their lactation periods. Some difficulty was anticipated with cow AC due to her high milk yield at the time (35 lb. per day) and so her food consumption was restricted for 5 days. This may have helped.

Milk was sampled on one day every week and analysed for total solids, fat, protein and lactose, (ash by difference). Milk composition was found to vary greatly among the cows and total yields were calculated to the 4 percent fat-corrected basis. This was not done by the simple application of Gaines's (1928) formula, F.C.M. = 0.4M + 15F, as the fat percentages in AC's and BC's milk were below 2.6 percent, the lowest value in the range of values used by Gaines for calculating his regression equation. The protein and lactose contents of these cows' milks were also possibly outside Gaine's ranges. The total amounts of fat, protein and lactose were first calculated, and then the energetic equivalents of these amounts were calculated using the factors 4132, 2659 and 1792 kcal./lb. of fat, protein and lactose respectively (Anderson 1926). These energy values were added to give the total milk energy production which was converted to the 4% F.C.M. basis by dividing by the energy content of one lb. of 4 percent F.C.M. (340 kcal.).

Determination of dry-matter digestibility

Single 12-day digestibility trials were carried out before, during and after lactation with each cow in Experiment 2 (Trials 1, 2 and 3 respectively). Food dry-matter digestibility was calculated from estimates of food dry matter intake and faeces dry matter output over the 12 days. Samples of the food offered, food left and faeces produced were obtained on each of the 12 days and their dry matter percentage determined by oven drying at 100 degrees. These were used to estimate the amounts of food dry matter offered and left and the faeces dry matter

produced. Faeces were collected on plywood sheets which were fitted into the stalls (Photograph 3). They were sloping so that urine drained away. When the animals were taken from their stalls, they were tied separately so that any dung produced could be scraped up from the floor. Dung produced in the byre was picked up from the gutter. The animals were followed with a shovel when being moved over open ground between the shed and weighing room or byre.

Determination of rate of passage

The rate of passage of undigested residues through the alimentary tract was determined in conjunction with the digestibility trials. The animals were given small amounts of stained food and the numbers of stained particles occuring in the faeces collected at regular intervals afterwards were counted. The procedure is a modification of that used by Balch (1950). It was developed during the course of these trials when it was found initially that some features of the existing procedure were unsatisfactory; it was thus developed at the expense of obtaining valid estimates of rate of passage for cows AH and AC for the first two trials.

Stains and staining procedure

From the hay, only stems, stripped of their leaves and seed heads, were stained. It was found that this material gave fewer specks and hair-like particles in the faeces than whole stems; such specks and hair-like particles make counting more subjective and undoubtedly increase counting errors. From the concentrate mixture the rolled oats were sieved off for staining. The

selected materials were stained with Safranine (TN 125), Brilliant Green (YNS crystals) and Methyl Violet (10 BNS), all supplied by Imperial Chemical Industries, Ltd., by boiling them for one hour in 0.1 percent (0.05 percent for Methyl Violet) solutions and then washing them with hot and cold tap water until the washings were colour-free. They were then dried at 100 degrees C. overnight. It was found in the course of the determinations that material stained with Safranine passed consistently more quickly than that stained with either Brilliant Green or Methyl Violet. This is shown in Figure 3. Such a difference between stains does not seem to have been reported before. The possibility of different rates of passage for different stains was recognised by Castle (1956)(she found no difference in this respect between Brilliant Green and Basic Fuschin with pigs), though apparently not by other investigators. Balch (1950) reported that the breakdown of stained particles in the reticulo-rumen was probably slower than that of the original food. It is reasonable to suppose that this slower breakdown was equally pronounced with Brilliant Green and Methyl Violet because they are closely related chemically and more so for both of these than for Safranine from which they differ chemically (Imperial Chemical Industries, Ltd., 1962).

Administration of stained material

Difficulty was encountered in obtaining voluntary consumption of the stained material, even when it was mixed with untreated food. The stained material from concentrates was therefore put

into paper capsules which were administered with a dosing gun. This method had the advantages of exact control of the "time of eating," and provided a means of getting stained material into the reticulo-rumen at times of the day when the animals would not eat even the untreated food. The rate of passage curves obtained with capsule-administered material were the same shape as those obtained when the material was eaten normally in two comparisons, but the overall rate of passage of capsule-administered material may have been slower than that of material eaten by the cow.

It was found that stained material from hay could be successfully administered (slightly moistened with a sugar solution) by forcing small amounts of it into the animal's mouth. Once there, it was chewed and swallowed in a normal manner.

A single dose of stained material was 100 g. for the concentrates (5 capsules of 20 g. each) and 80 g. for the hay.

In the second and third trials with BH and BC 2 or 3 differently-coloured doses were given at different times of the day on successive days. The colours and times were rearranged in every trial. In the third trial with AH and AC 3 differently-coloured doses were combined and given at one time, 9 AM.* In this way the following points were brought out (Figure 3):

*The amount of material of each colour was only one-third the usual dose; the combined amount was equivalent to an ordinary single dose of 80 or 100 g. With cow AC the total number of particles of each colour was very small and the usual counting errors were greatly magnified as is evident from the abnormal shapes of the curves.

1) Safranine-stained material had a faster rate of passage than that stained with either Brilliant Green or Methyl Violet.
2) The time of administering the dose had no effect on the rate of passage.

Collection of faeces

In the first two trials, faeces were collected at 6-hour intervals for 5 to 6 days and then at longer intervals, never exceeding 24 h. It was decided, however, that this frequency was unnecessarily high. In the third trial, the interval was increased to 12 h. for the cows consuming hay and 24 h. for those consuming concentrates. The data from the first two trials were then re-plotted on the same basis. Collection times in the third trial were 9 AM and 9 PM; when stained food was given at times other than 9 AM, the first collection in which stained particles appeared was sometimes 24 or 36 hours (for hay and concentrates respectively) after administration.

Particle counting procedure

Stained particles were counted daily in the fresh faeces. A half-pint sample of each collection was obtained. From this 3 or 4 subsamples of 12 g. were weighed out. These were transferred to an ordinary bowl-shaped kitchen sieve and washed with 2 l. of water delivered by gravity from an elevated bottle (see Photograph 4). A constant pattern of movement of the stream of water so delivered was followed. With this washing procedure, no advantage in precision was found in expressing particle counts in terms of the dry weight of material remaining after washing, the standard procedure of Balch (1950). The residue on

the sieve was then transferred, by means of a gentle stream of water to a square of nylon cloth. The cloth was placed on a glass plate and illuminated from below through cross-ruled tissue paper by a lamp.

Precision

An idea of the precision of this method may be obtained by comparing the green and blue curves in the several trials. In no case (except with AC in the third trial) did the 'R' values (see next section) differ by more than 2 h.

Analysis of data

The usual excretion curves (Balch, 1950) were drawn and are presented in Figure 3. From these, 'R' values (Castle, 1956), estimating the average time of retention of indigestible particles, were calculated. Comparable 'R' values were then used to estimate changes in the average alimentary content of indigestible dry matter from one trial period to another, by means of the formula

$$C = I \cdot R.$$

This formula has been used by Makela (1956) to estimate the average retention time of a dry-matter "point" ('R', in days) from measured daily dry-matter intake ('I', in pounds) and alimentary dry-matter content ('C', in pounds) determined at slaughter. Beginning with 'R', the average time of retention of an indigestible dry matter point, as estimated by Castle's 'R' values (expressed in days) obtained in these trials, the calculation has been carried out in reverse to obtain an estimate of 'C', the average alimentary content of indigestible dry matter, in pounds. The average daily intake of indigestible dry matter,

in pounds, ('I') was calculated from estimated dry-matter intake and the indigestibility coefficient of the dry matter. The value for 'C' will, of course, fluctuate around the mean during the course of a day as 'I' and 'R' are not constant rates.

Exercise

An exercise treatment was begun with X and Y in the fourth month of Experiment 1. It consisted of leading the cows at a brisk walking pace behind a farm tractor over a standard course. This treatment was not successfully carried out and was abandoned after four weeks.

Sampling of rumen fluid

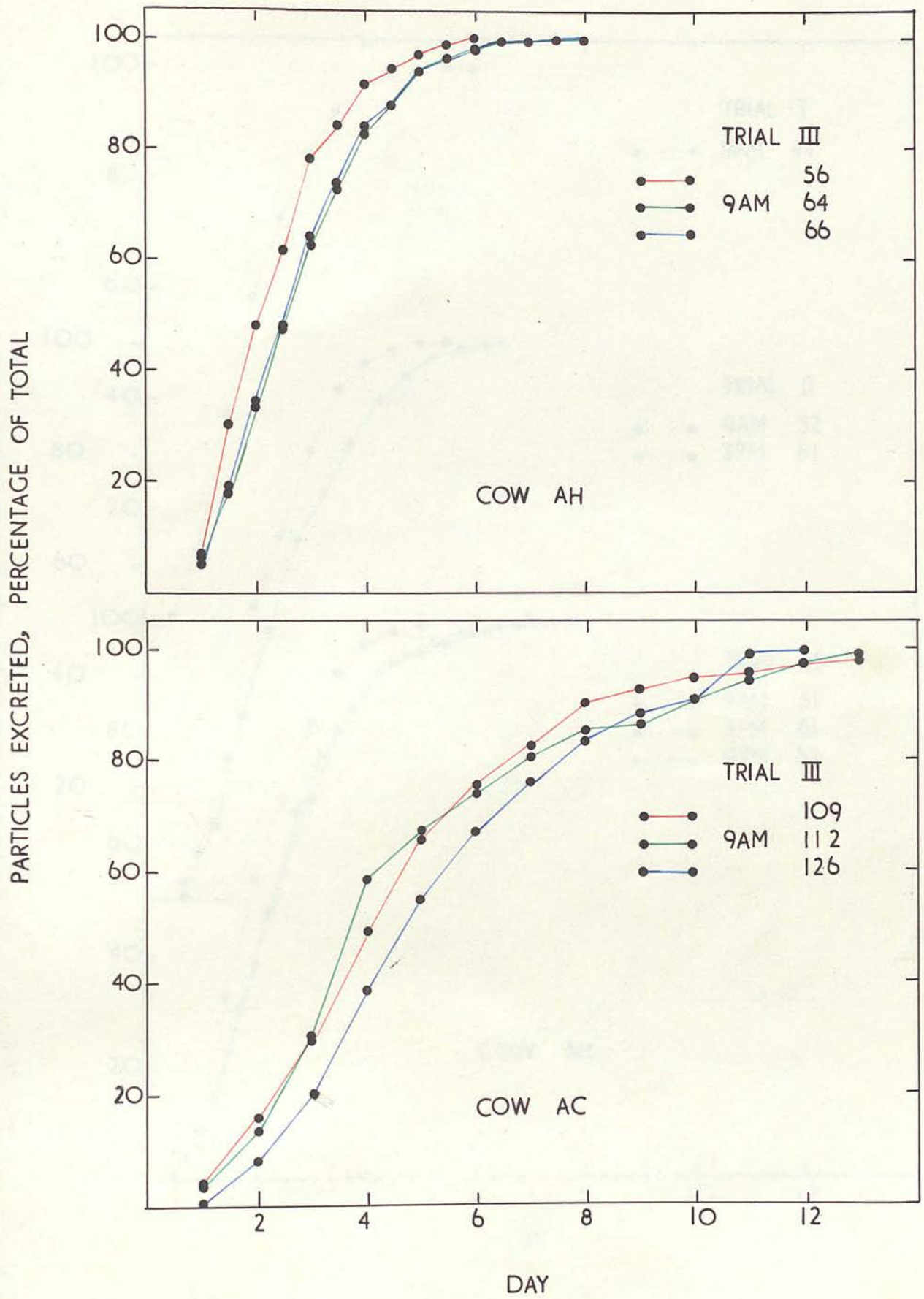
Rumen fluid samples were obtained by stomach tube at various times during the day on two occasions from cow AC and on one occasion from cow AH. The samples were collected in 4-ounce, glass, screw-topped jars interposed between the stomach tube and the pump. Samples were cooled immediately under cold tap water for 5-10 minutes and then in a deep-freeze at -8 degrees C. for 1-2 h. They were then held, for not more than 24 h., at just above 0 degrees. They were allowed to warm up to room temperature before their pH was determined electrometically with a 'Pye' meter.

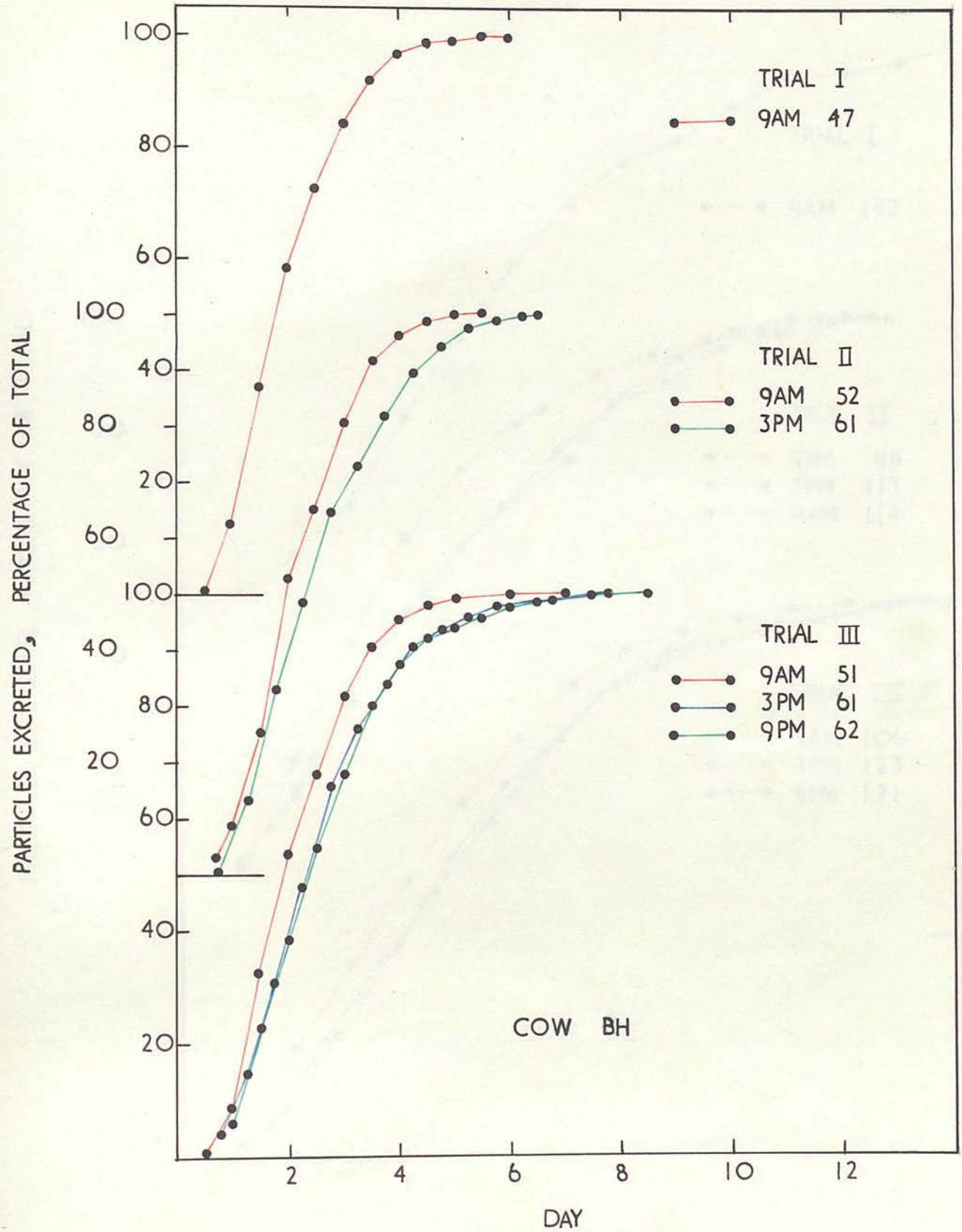
2. Results

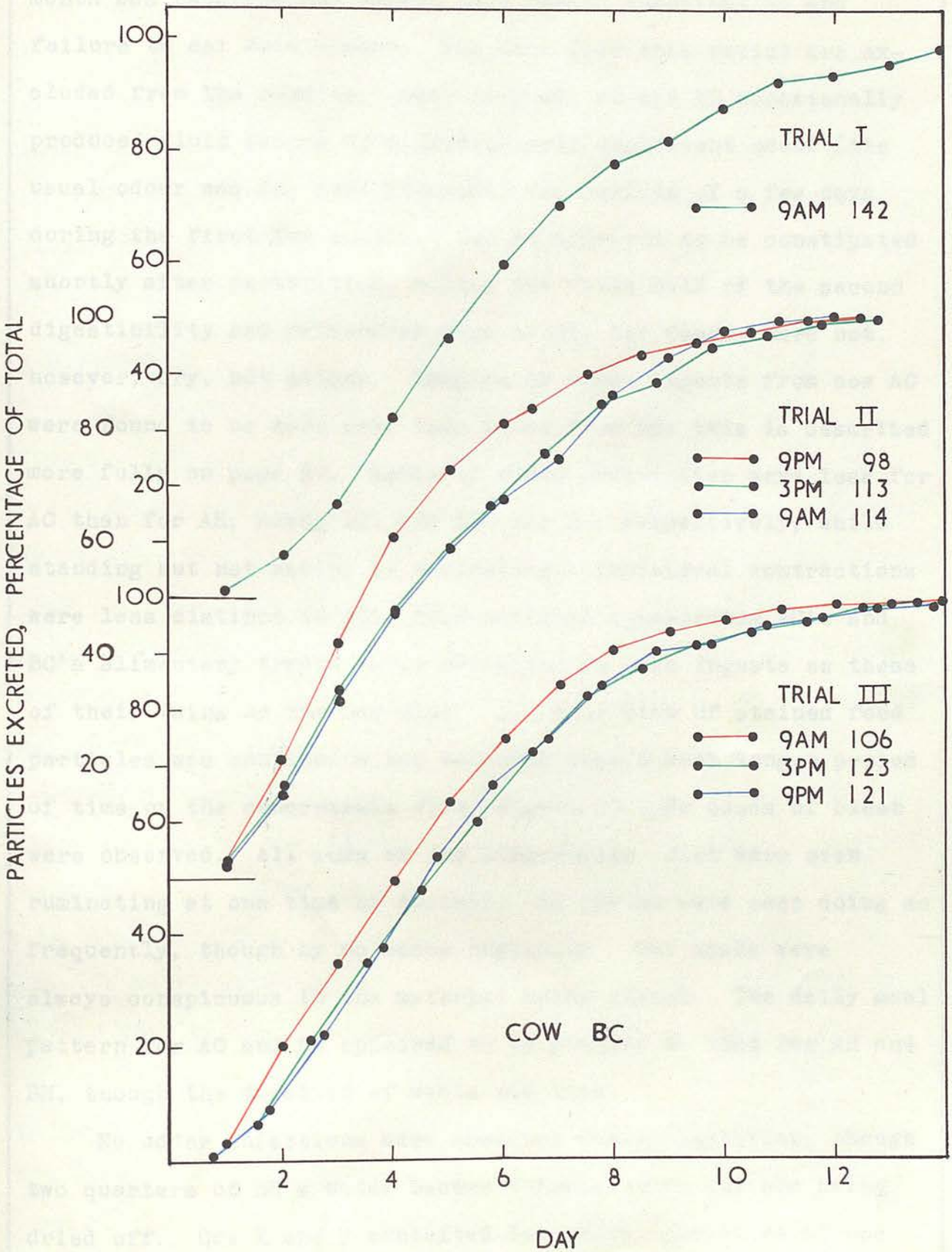
General observations

A period of adjustment to the concentrate diet of up to one

Figure 3. Rate of passage curves. The times are those at which variously-stained materials were administered and are followed by 'R' values in hours. Note that stained material of all colours was mixed and administered simultaneously to cows AH and AC in Trial III.


PARTICLES EXCRETED, PERCENTAGE OF TOTAL
100
80
60
40
20
TRIAL III
9AM
56
64
66
COW AH
100
80
60
40
20
TRIAL III
9AM
109
112
126
COW AC
2
4
6
8
10
12
DAY


PARTICLES EXCRETED, PERCENTAGE OF TOTAL
100
80
60
100
40
80
20
60
100
40
80
20
60
40
20
2
4
6
8
10
12
DAY
TRIAL I
9AM 47
TRIAL II
9AM 52
3PM 61
TRIAL III
9AM 51
3PM 61
9PM 62
COW BH


PARTICLES EXCRETED, PERCENTAGE OF TOTAL
DAY
TRIAL I
9AM 142
TRIAL II
9PM 98
3PM 113
9AM 114
TRIAL III
9AM 106
3PM 123
9PM 121
COW BC

month was required and during this period constipation and failure to eat were common. The data from this period are excluded from the results. Once adapted, AC and BC occasionally produced fluid faeces of a particularly unpleasant odour (the usual odour was far from pleasant) for periods of a few days during the first few months. Cow AC appeared to be constipated shortly after parturition, during the first half of the second digestibility and rate-of-passage trial; her faeces were not, however, dry, but sticky. Samples of rumen ingesta from cow AC were found to be more acid than those from AH; this is described more fully on page 87. Rates of rumen contraction were less for AC than for AH, being 111 and 130 per h., respectively, while standing but not eating or ruminating. Individual contractions were less distinct in AC. From external appearances AC's and BC's alimentary tracts never contained as much ingesta as those of their twins on the hay diet. The excretion of stained food particles was continuous and occurred over a much longer period of time on the concentrate diet (Figure 3). No cases of bloat were observed. All cows on the concentrate diet were seen ruminating at one time or another; AC and BC were seen doing so frequently, though by no means regularly. Oat husks were always conspicuous in the material being chewed. The daily meal pattern for AC and BC appeared to be similar to that for AH and BH, though the duration of meals was less.

No udder infections were observed during lactation, though two quarters of BH's udder became infected when she was being dried off. Cow X and Y exhibited low-grade infections of one or more quarters on several occasions. All these infections

were successfully treated with antibiotic prepartions.

Cow Y, on one occasion during the seventh month of Experiment 1, exhibited symptoms of hypomagnesemia. She recovered immediately after receiving an injection of magnesium salts. Analysis of a blood sample taken at the time, however, gave normal serum levels of calcium, inorganic phosphorus and magnesium (10.2, 4.7 and 2.3 mg./100 ml., respectively).

Experiment 1

The food consumption and body weights of cows X and Y in Experiment 1 are given in Figure 4 as means of 10-day intervals. Daily values are given in Appendix Table 1. Both cows increased in weight until they reached constant weights of approximately 1500 lb. at 60 days and 1250 lb. at 35 days respectively. These weights were maintained until the onset of the exercise treatment. Cow X was a slightly larger-framed animal than Y, but in addition was considerably more obese at her constant weight. The effect of exercise was to decrease body weight. When the exercise was discontinued, weights increased again until the previous constant weights were regained at about day 260 for X and day 300 for Y and these have been maintained up to the time of writing. The rate of increase in weight after the exercise was slower and less steady than before. Cow Y maintained a constant weight of 1150 lb. for about two months during this interval. Except for the initial period of recovery from the exercise, food consumption was greater during periods when body weight was increasing than when it was stable. This was most clearly shown by Y; the establishment of a constant weight before the exercise, and

again between days 190 and 230, was accompanied by a reduction in food consumption to about 10 lb. A similar reduction was observed with X between days 260 and 300, but not before the exercise. The low average food intake by X between days 180 and 190 are the result of a complete refusal to eat on several days. Food consumption declined sharply during the exercise treatment; the reduction was more delayed with Y than with X, and Y's food consumption also recovered more slowly after the exercise was discontinued. The variability of daily food consumption throughout the course of the experiment was greater for X and Y than for the other cows on the concentrate diet (Table 4).

Both cows usually became very tired when exercised and on several occasions, in spite of what was thought to be a suitably gradual imposition of the treatment, they reached the limits of their endurance. For Y this limit was apparently lower than for X as it was more often reached. Perhaps for this reason Y developed muscular weakness in her hind legs. When both animals developed sore feet (the soles of their feet wore thin), the exercise was discontinued.

Experiment 2

The results of Experiment 2 are given in Figure 5 and Appendix Table 1.

Cow AC did not gain weight during her period of adjustment to the concentrate diet and thus her first weight to be entered in Figure 5 was 20 lb. below AH's first weight, AH having continued to gain steadily over the adjustment period. AC gained more rapidly up to parturition, however, and was 20 lb. heavier

than AH at this time. She was also 20 lb. heavier immediately after parturition. AH's and AC's calves weighed 92 and 89 lb. respectively. Cow AH lost considerably more weight and over a longer period of time than AC. After lactation both cows gained weight, AC more rapidly than AH. When the supply of hay no. 3 was exhausted, AH was removed from the experiment. AC continued to gain weight at a steadily decreasing rate until she was removed from the experiment.

During the uniformity trial AH and AC consumed an average of 29.9 and 31.7 lb. of hay a day respectively; the difference between these means is not significant at the 5 percent level of probability. Their food consumption decreased considerably when they were changed from the hay diet of the uniformity trial to their experimental diets and this was more marked with AC, on the concentrate diet, than with AH. The food consumption of both cows increased after parturition, AH's more rapidly than AC's. AH then maintained a fairly uniform level of consumption to the end of the experiment. During lactation AC also maintained a higher average level of consumption (Table 5). Consumption did, however, tend to decline from the beginning to the end of lactation. Consumption was again high early in her post-lactation period and decreased gradually until a constant level of about 22 lb. was established at about day 280.

Two troughs are conspicuous in AC's food consumption curve, one between days 20 and 80 and another between days 190 and 210. During the peak periods of consumption on either side of these troughs AC appeared to be in pain at various times of the day, but especially following her usual period of heavy eating from

9:00 to 9:30 or 9:45 AM. She was restless, breathed heavily, pressed her nose against the stall, closed her eyes and sometimes ground her teeth together. Rumen motility was apparently absent at this time. These symptoms were never observed at lower levels of consumption except on a few occasions before parturition. Levels of consumption above 28 lb. a day were not maintained for more than about 15 days at a time and were followed by sharp falls in consumption. It was thought that she might be suffering as a result of high acidity of her ruminal contents. Two sets of rumen fluid samples were therefore obtained, one during a period (day 214 - 227) when these symptoms were regularly seen and the other when they were not (day 278 - 281). The pH values of these samples are plotted in Figure 6. During the first period, the pH always dropped within one hour after she began eating by about a pH unit to 5.5 - 5.7, corresponding to the onset of her distressed condition. It remained below 6.0 most of the day. During the second period, on the other hand, no such sharp fall was found and only one sample gave a pH value below 6.0.

AC produced approximately one gallon of milk a day more than AH, but owing to the lower energy content of her milk the yields of 4 percent fat-corrected milk were nearly the same for both (Table 7). AC's milk production curve, in addition to the depression corresponding to the depression in the food consumption curve, appears, from a comparison with the other cows' lactation curves, to be abnormal in not having a fully developed peak.

Food consumption, body weight and milk production patterns

for BH and BC were similar to those for AH and AC. They gained more weight than AH and AC before parturition, gaining at similar rates but over longer periods of time. After day 40 BC maintained a fairly constant weight of 1150 lb. until day 220. She then increased slowly to about 1270 lb., a weight which she then more-or-less maintained to the end of the experiment. BH continued to lose weight until day 80 and then after lactation gained until she nearly equalled BC in weight when she was removed from the experiment.

Cow BH's food consumption curve shows a slight peak between days 50 and 60 in contrast to AH's level consumption curve after parturition. BC's average daily food consumption during lactation was only slightly higher than before parturition (Table 5). Her food consumption decreased quickly after lactation to a level of about 16 lb. a day. After day 270 it increased slowly along with body weight and again decreased, to 16 lb., when a constant body weight was re-established. The depression in her level of food consumption and the associated depressions in body weight and milk production between days 30 and 50 is thought to be due to an inadequate salt intake; the symptoms of distress observed with AC were never observed with her. With the onset of lactation her appetite for salt increased and through negligence her daily salt allowance was not increased. A very strong craving for salt was noticed about day 45 and was gradually satisfied over a period of several days.

The results of the digestibility and rate-of-passage trials are given in Table 6. The rate-of-passage curves are presented

in Figure 3. The outstanding feature of these data is that the increased food consumption after parturition was accompanied by an increased rate of passage (smaller 'R' value) with cow BC but a slightly decreased rate of passage (larger 'R' value) with cow BH.

A complete record of milk composition is given in Appendix Table 2. The weighted means for the entire lactation period are given in Table 7 along with lactation and average daily yields of 4 percent fat-corrected-milk.

3. Discussion

General observations

The absence of rumination on the concentrate diet, the slower rate of passage of its undigested residues, the reduced amount of ingesta in the reticulo-rumen, the reduced rate of ruminal contraction and the lower pH values of rumen fluid are all in agreement with the observations of those who have investigated the reaction of the cow to a diet composed largely or entirely of concentrates.

With the hay diet consumed by cows AH and BH the rate of passage of undigested residues was determined by the rate of digestion of the hay dry matter in the reticulo-rumen (cf. page 54). This was not the case with the concentrate diet consumed by X, Y, AC and BC, because the rate of passage would then have been faster and not slower than it was with the hay diet; rather, the rate of passage was probably determined by the need to maintain a minimum amount of ingesta in the reticulo-rumen.

Figure 4. Food consumption and body weight of cows X and Y in Experiment 1. Each point is the mean of ten consecutive daily values in pounds.

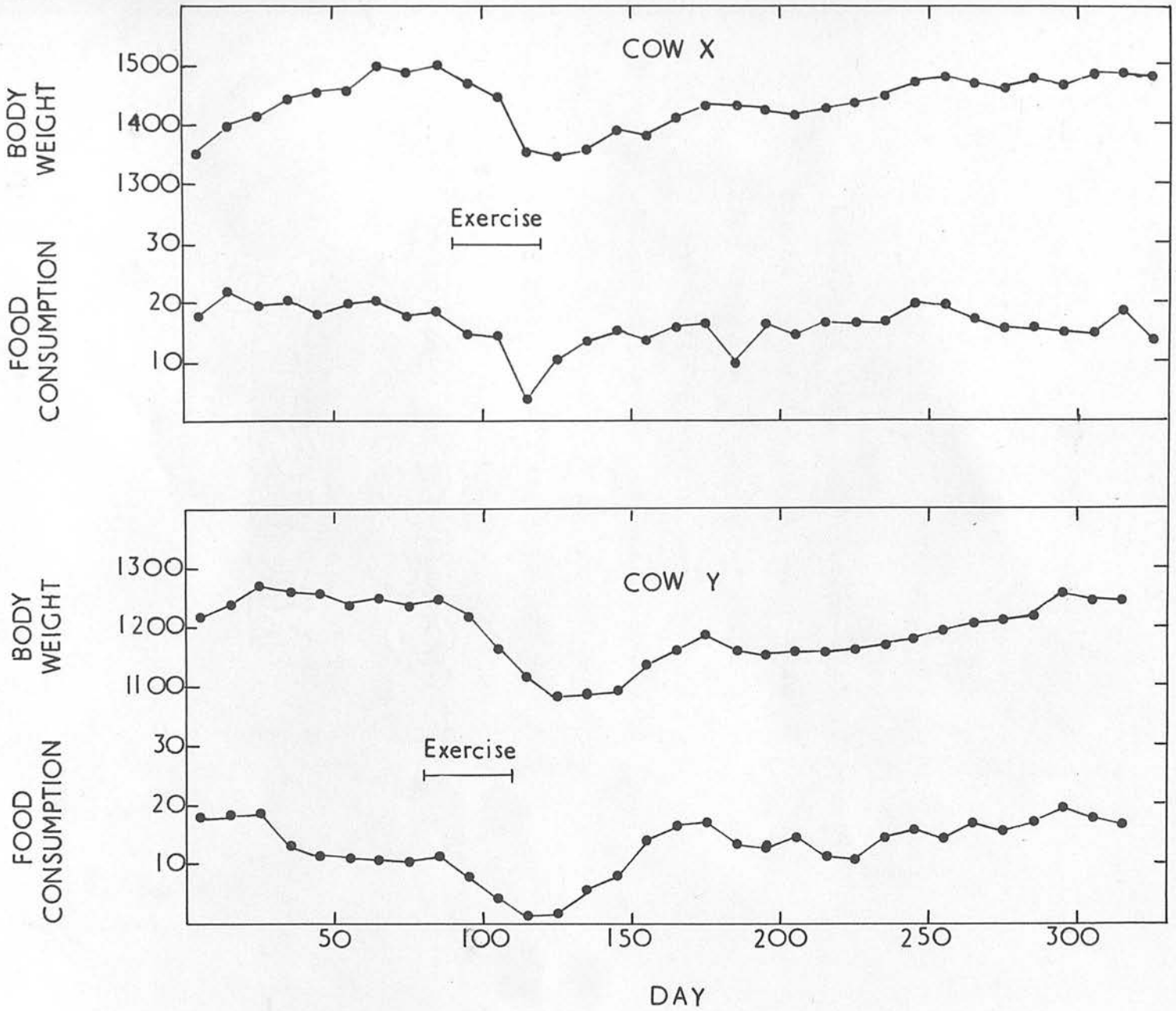
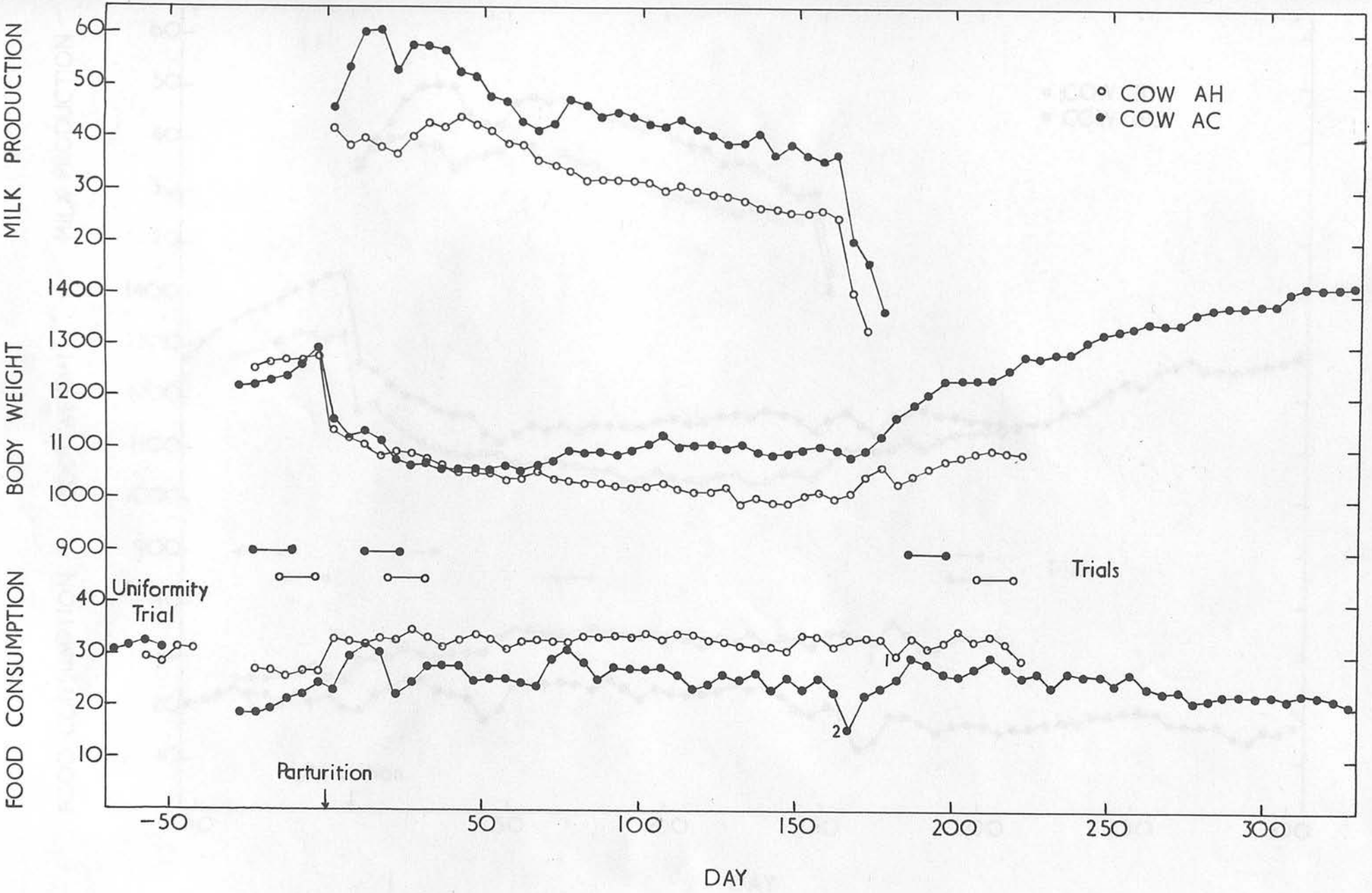
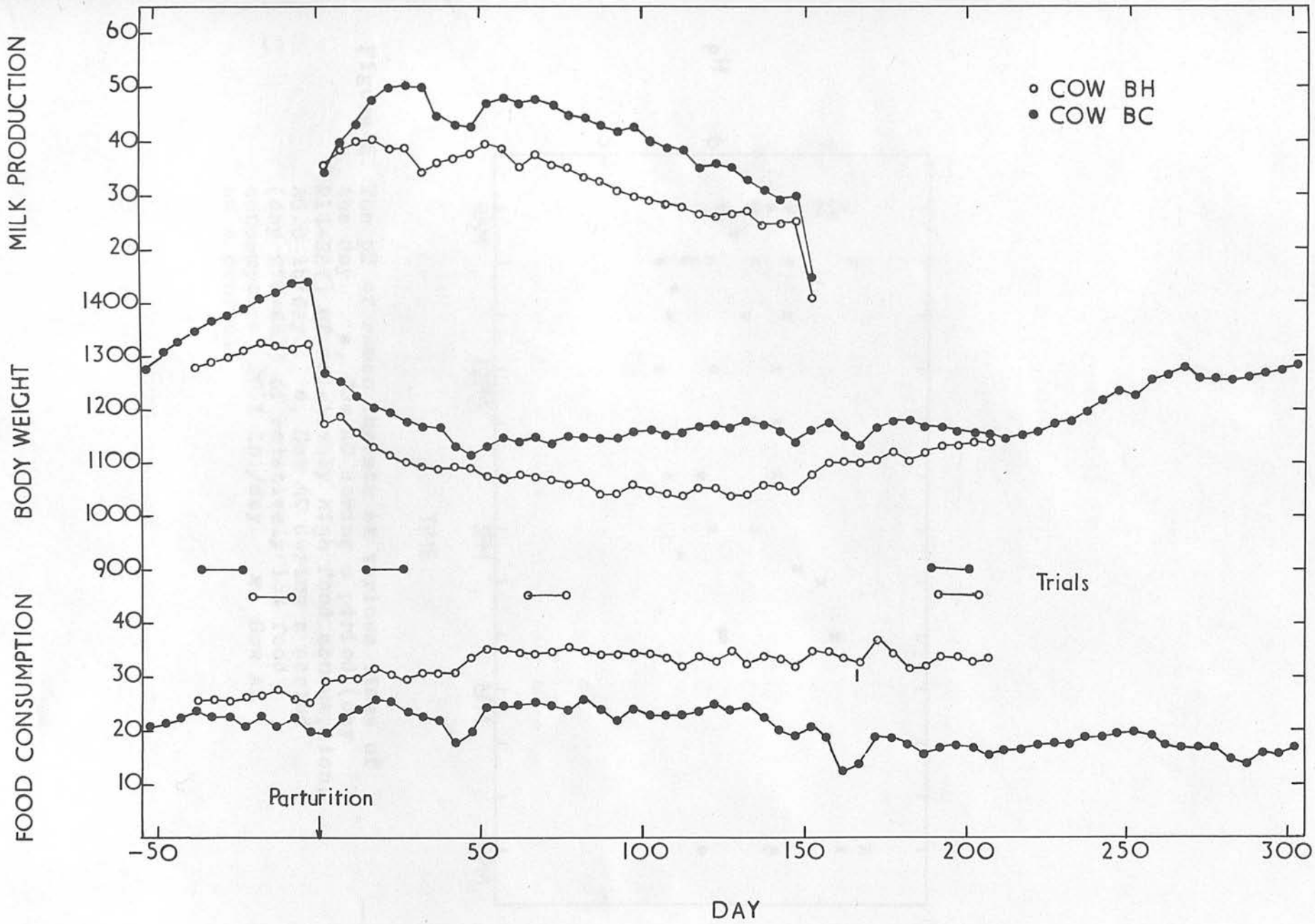

COW X
BODY WEIGHT
1500
1400
1300
Exercise
FOOD CONSUMPTION
30
20
10
COW Y
BODY WEIGHT
1300
1200
1100
Exercise
FOOD CONSUMPTION
30
20
10
50
100
150
200
250
300
DAY

Figure 5. Food consumption, body weight and milk production of cows AH, AC and BH, BC in Experiment 2. Each point is the mean of five consecutive daily values in pounds. Notes: 1. Cows AH and BH were switched from hay no. 2 to hay no.3 during these periods (cf. page 60). 2. Cow AC's food consumption was restricted during this five-day period as an aid to drying her off (cf. page 72).


MILK PRODUCTION
BODY WEIGHT
FOOD CONSUMPTION
COW AH
COW AC
Uniformity Trial
Trials
Parturition
DAY
60
50
40
30
20
1400
1300
1200
1100
1000
900
40
30
20
10
−50
50
100
150
200
250
300
1
2


MILK PRODUCTION
BODY WEIGHT
FOOD CONSUMPTION
60
50
40
30
20
1400
1300
1200
1100
1000
900
40
30
20
10
COW BH
COW BC
Trials
Parturition
-50
50
100
150
200
250
300
DAY

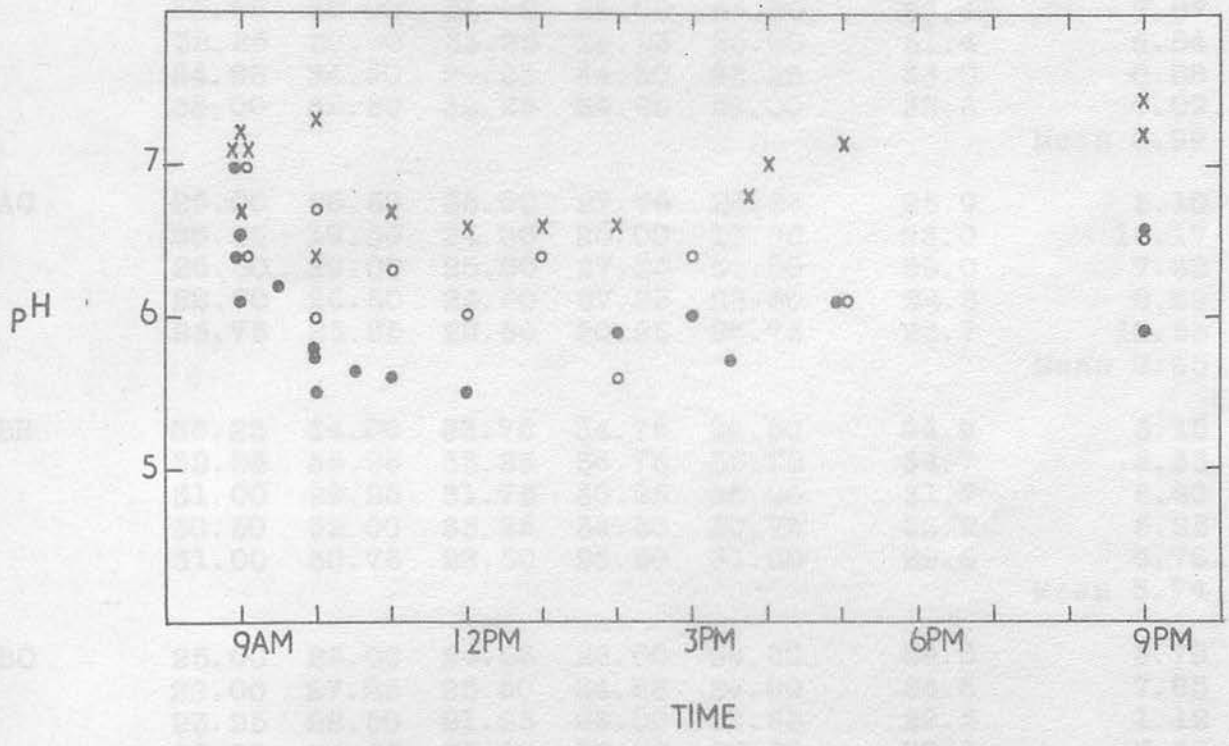


Figure 6. The pH of rumen ingesta at various times of the day. ●, Cow AC during a period (day 214-227) of relatively high food consumption, 26.8 lb/day. o, Cow AC during a period (day 276-281) of relatively low food consumption, 20.1 lb./day. ×, Cow AH as a control.

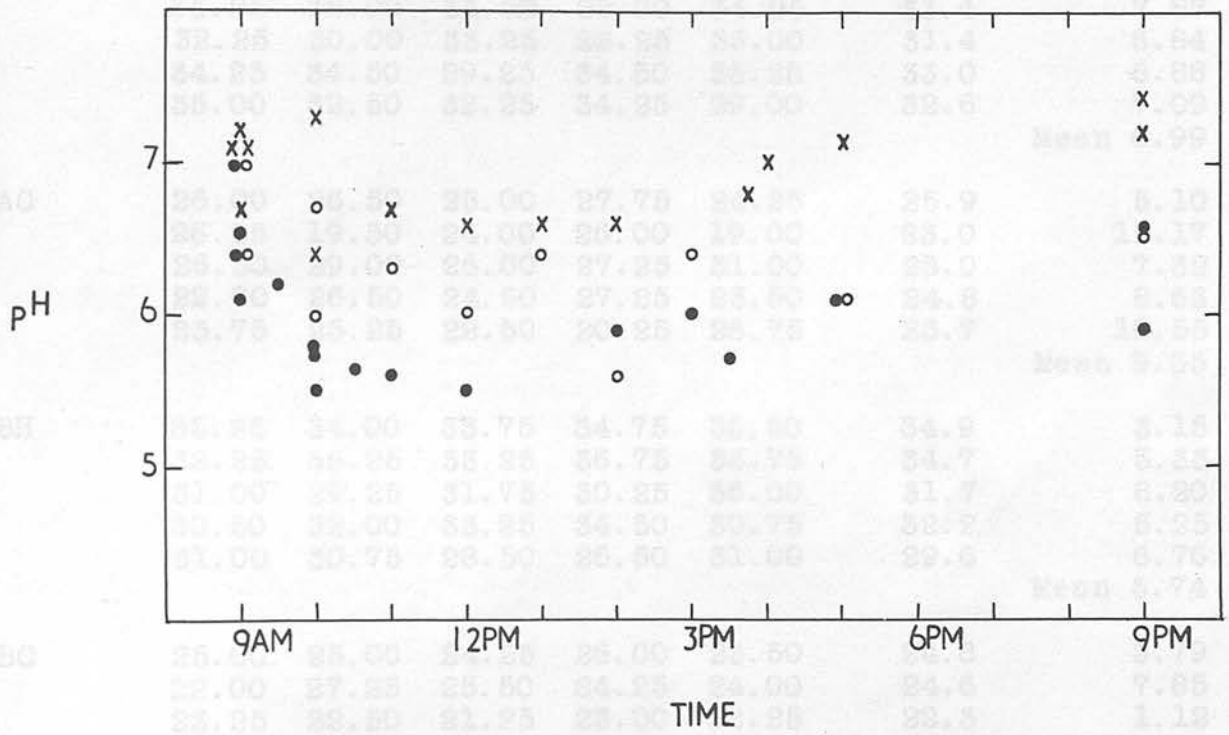

pH
7
6
5
9AM
12PM
3PM
6PM
9PM
TIME

Table 4. Variation in daily food consumption within randomly selected 5-day periods shown by cows X and Y in Experiment 1 and by cows AH, AC, BH and BC in Experiment 2.

	Food Eaten (lb.)						
	Day of period						Coeff. of Variation
COW	1	2	3	4	5	Mean	(%)
AH	31.50	33.00	31.00	33.75	36.75	33.1	6.28
	33.25	36.00	34.50	29.00	34.25	33.4	7.87
	32.25	30.00	33.25	28.25	33.00	31.4	6.84
	34.25	34.50	29.25	34.50	33.25	33.0	6.88
	35.00	32.50	32.25	34.25	29.00	32.6	7.09
						Mean	6.99
AC	26.00	26.50	25.00	27.75	24.25	25.9	5.10
	26.25	19.50	24.00	26.00	19.00	23.0	15.17
	26.50	29.00	26.00	27.25	31.00	28.0	7.32
	22.00	26.50	24.50	27.25	23.50	24.8	8.63
	23.75	25.25	22.50	20.25	26.75	23.7	10.55
						Mean	9.35
BH	35.25	34.00	33.75	34.75	36.50	34.9	3.15
	32.25	35.25	33.25	36.75	35.75	34.7	5.33
	31.00	29.25	31.75	30.25	36.00	31.7	8.20
	30.50	32.00	33.25	34.50	30.75	32.2	5.25
	31.00	30.75	28.50	26.50	31.00	29.6	6.76
						Mean	5.74
BC	25.00	25.00	24.25	26.00	23.50	24.8	3.79
	22.00	27.25	25.50	24.25	24.00	24.6	7.85
	23.25	22.50	21.25	23.00	22.25	22.3	1.12
	22.50	24.25	21.50	19.75	22.50	22.1	7.47
	23.75	24.00	23.00	23.00	26.50	24.1	5.98
						Mean	5.24
X	15.25	14.25	6.00	15.50	16.50	13.5	31.63
	17.00	20.50	15.25	17.00	16.25	17.2	11.51
	19.00	19.25	22.75	21.50	23.00	21.1	8.86
	20.25	15.00	21.75	23.25	20.25	20.1	15.47
	18.75	19.00	10.00	18.50	18.00	16.9	22.78
						Mean	18.05
Y	14.00	15.50	13.25	7.75	11.50	12.4	24.00
	11.25	18.25	11.75	9.00	9.25	11.9	31.51
	15.50	16.25	14.75	17.50	17.50	16.2	7.53
	6.00	4.50	11.00	9.25	14.75	9.1	39.89
	14.50	11.50	9.00	14.25	8.50	11.6	24.31
						Mean	25.45

Table 5. Average daily food consumption before, during and after lactation by cows AH, AC, BH and BC in Experiment 2, in pounds.

Cow	Before	During	After	
		(day 1-165)	(day 181-225)	(day 226-305)
AH	26.4	32.7	32.0	-
AC	21.6	26.4	27.5	23.4
" (hay equivalent)*	36.7	44.9**	46.8	39.8
		(day 1-150)	(day 156-210)	(day 211-305)
BH	26.1	32.7	33.4	-
BC	21.3	22.9	16.2	17.0
" (hay equivalent)*	36.2	38.9	27.5	28.9

*The hay equivalent of 1 lb. of concentrates is 1.7 lb., i.e., the starch equivalent value of the concentrates is $\frac{65}{38}$ = 1.7 times that of the hay.

**The hay equivalent of AC's highest level of consumption, 31.9 lb/day between days 10 and 15, is 54.2 lb., or about 60 percent more than AH consumed at any time during lactation.

Table 6. Dry-matter intake, dry-matter digestibility and values of 'R' and 'C' for cows AH, AC, BH and BC for three different periods during Experiment 2.

Cow		Trial I (before parturition)	Trial II (during lactation)	Trial III (after lactation)
AH	D.M. intake, lb.	22.2	27.8	28.2
	D.M. digest., %	64.8	63.8	66.2
	R value, hr.*	-	-	56
	C value, in lb.	-	-	23
AC	D.M. intake, lb.	16.6	24.7	23.8
	D.M. digest., %	76.0	74.6	73.0
	R value, hr.**	-	-	126
	C value, lb.	-	-	34
BH	D.M. intake, lb.	22.6	29.0	28.9
	D.M. digest., %	64.8	62.8	66.8
	R value, hr.*	47	52	51
	C value, lb.	16	24	20
BC	D.M. intake, lb.	18.9	21.3	14.2
	D.M. digest., %	77.1	76.3	70.1
	R value, hr.**	142	113	123
	C value, lb.	25	24	22

*Red excretion curves (figure 3) compared.

**Green excretion curves (figure 3) compared.

Note: Hay 2 was consumed by AH and BH during Trial periods I and II, hay 3 during period III.

Table 7. Yields and composition of milk from cows AH, AC, BH and BC during 150-day lactations in Experiment 2.

Cow	Milk yield (lb.)	Fat	S.N.F.	Protein	Lactose	Ash	Yield of 4% F.C.M., total (lb.)	Yield of 4% F.C.M., average daily (lb.)
			(percentage)					
AH	5150	3.95	8.23	3.04	4.61	0.58	4947	33.0
AC	6878	1.94	8.94	3.26	4.96	0.72	5172	34.5
BH	4843	3.82	8.64	3.13	4.98	0.53	4705	31.4
BC	6115	2.33	9.13	3.40	5.01	0.72	4972	33.2

According to Scheunert and Trautmann (1951) one of the requirements for onward passage of ingesta is a minimum degree of filling of the reticulo-rumen. Certainly the reticulo-rumen never empties, and, indeed, even severe restrictions in the amount of food an animal eats and fasts do not greatly reduce the amount of ingesta it contains. Under these conditions there are marked reductions in the rate of passage (Makela, 1956). The explanation for this may be largely anatomical in that ingesta may overflow out of the ventral rumen only as newly ingested food is added. The reduced rate of reticulo-ruminal contraction, observed in these experiments and by Balch, Balch, Bartlett, Bartrum, Johnson, Rowland and Turner (1955), may be a contributory factor to the extent that it indicates a reduction in the total forces acting to move ingesta out of the reticulo-rumen. The reduced amount of ingesta in the reticulo-rumen obvious in these experiments, and confirmed by direct measurement by Balch *et al.* (1955), and the constancy of BC's alimentary content of indigestible dry matter ('C') in these trials also favour this hypothesis of Scheunert and Trautmann.

A diet containing little or no hay is consumed more rapidly and ruminated less than normal, mixed or all-hay diets (Balch *et al.*, 1955). The reduction in the amount of chewing performed results in a reduction in the daily amount of saliva flowing into the reticulo-rumen, the rate of saliva secretion being several times greater during chewing than otherwise, and thus a proportionate reduction in the amount of buffered alkali added to the reticulo-ruminal contents (Bailey and Balch, 1961;

Bailey, 1961). The lowered neutralising capacity of the reticulo-ruminal fluid results in a lower average pH, a pH below 6.0 rather than above (Balch et al., 1955; Balch and Rowland, 1957). A combination of the lower pH and the change in the predominant carbohydrate of the diet from cellulose to starch causes changes in the generic composition of the microbial population of the reticulo-rumen and thus in the course and end-products of the fermentation of dietary carbohydrate (Balch and Rowland, 1957). The concentration of total steam-volatile fatty acids are more variable during the day, rising to higher levels after meals and falling to lower levels before meals; the pH also fluctuates more. Lactic acid, which appears to be an intermediate in the fermentation of starch to volatile fatty acids (Phillipson, 1952), often accumulates briefly during the first few hours after a meal, indicating that the rate of its production is greater than the rate of its conversion to volatile fatty acids. Also, the relative molar proportions of acetic, propionic and butyric acids change from about 4:2:1, respectively, to about 2:2:1.

Sodium bicarbonate was added to the concentrate mixture in order to raise somewhat the neutralising capacity of the reticulo-ruminal fluid. Whether it was needed or not is not known. The results of an early investigation of all-concentrate diets suggested that it was very beneficial for growing animals, i.e., they ate more food and gained weight faster when it was added to their food (Preston et al., 1961). In some of the more recent investigations, however, no benefit was found

(Nicholson, Cunningham and Friend, 1962; Preston, Whitelaw, MacLeod and Charleston, 1962).

Experiment 1

With cow Y in the first stage of this experiment, before the exercise, the obvious relationship between body weight and food consumption must have been a casual one with consumption being the dependent and weight being the independent variable. This is evident from a lack of evidence that any other factor could have been controlling consumption. Food consumption could have been determined by either Y's physical capacity for the food or indigestion such as AC suffered (cf. page 86) and its associated discomfort; no other alternatives come to mind. Since both AC and BC consumed 25 lb. of the same food per day quite comfortably for long periods of time, it does not appear probable that Y's consumption could have been limited to not more than 19 lb. by either of these factors. Moreover, these factors could only have imposed an upper limit to the level of consumption and could not have accounted for the decrease in Y's consumption from 19 to 11 lb. accompanying the establishment of her stable weight. She thus achieved and then maintained the weight of 1250 lb. by regulating her food consumption. The same behaviour is reported by Cowgill (1928) for dogs under a similar environment.

Cow X also demonstrated a stable body weight during the first phase of the experiment, but there is no clear-cut decrease in food consumption when it was achieved. The length of time between the attainment of this stable weight and the beginning

of the exercise was, however, probably insufficient for any such reduction to have become clearly manifest. Her pattern of food consumption following the attainment of the same stable weight after the exercise treatment does, however, make it fairly certain that such a reduction would have occurred.

With the exercise treatment it was the intention gradually to increase the amount until a level well out of any possible sedentary, non-responsive range (Mayer, 1954, 1955c; cf. page 30 was reached. It was thought that 10 miles, or 5 h. per day would be adequate and this was the goal set. Five miles, or 2.5 h. per day was the maximum reached. In spite of a gradual increase in the daily amount of exercise given, it became apparent during the last week that the rate of increase had been too great; they did not adapt themselves but rather became more exhausted every day. It appeared that the effect of this was primarily upon food consumption, the rapid fall in body weight resulting from very low food intakes; the loss of body weight continued for 10 to 20 days after the exercise was discontinued. The treatment was thus unsuccessful. It did not allow the (adapted) animals' reaction to exercise to be determined. Its net effect was essentially that of a fast.

After the exercise, Y increased to and then maintained a constant weight of 1150 lb. for about two months. As before the exercise, the attainment and maintenance of this constant weight was achieved by the regulation of food consumption. She began gaining weight again at the time of the attack of what appeared to be hypomagnesemia and what was, at any rate, successfully treated with magnesium salts. It is possible that this

successful treatment caused a resumption in body weight, or in other words that the condition that was successfully treated had gradually developed over the preceding two months and had been responsible for preventing further weight gain. Cow BC, however, behaved similarly at day 225 but suffered no such attack. Y has since day 300 possibly reached another period of stable weight, but further observation is necessary to confirm this.

Cow X returned, with a slight interruption between days 180 and 220, to nearly the same stable weight she maintained briefly before the exercise treatment. When this weight was reached, her food consumption decreased, thus confirming for X the regulation of food consumption which is so evident with Y. It is possible that this weight represents for X a "preferred" weight for these conditions, i.e., a weight which would be maintained indefinitely and to which she would always return after a period of fasting and body-weight loss (cf. page 32). A further period of observation is thought necessary to adequately examine this possibility.

Cows X and Y thus achieved and then maintained constant dry weights both before and after the exercise treatment by regulating their food intake to provide the necessary positive energy balance and then to maintain energy equilibrium. Whether or not they possess preferred weights is not at present certain and the cows will, therefore, continue to be observed. Their reaction to the exercise was a drastic decrease in food consumption which caused a decrease in dry weight. Their long term reaction, once they had become adapted to the exercise, was not determined but

would probably have been an increase in consumption and the maintenance of constant dry weights, at perhaps lower levels.

Experiment 2

Cows AC and BC

The amount of weight gained by BC before parturition was clearly more than could have been accounted for by the growth of the pregnant uterus. The uterine contents weighed 170 lb. at term and her weight gain was 160 lb. For AC the respective weights were 140 and 75 lb., but since the uterine contents of AH also weighed 140 lb. at term while her pre-parturition weight gain was only 20 lb., it is clear that AC's weight gain also represented an increase in the weight of non-uterine material. The possibility that this material was only or even largely extra-cellular water is ruled out by the fact that the cows' energy intakes were much larger than those of their twins. AC's and BC's average daily food intakes before parturition were 21.6 and 21.3 respectively; about 15.5 lb. would have supplied them with the same amount of net energy as AH and BH obtained from the 26 lb. of hay they ate daily. It is therefore concluded that AC and BC made large gains in dry weight before parturition.

After parturition the body weights of both cows decreased rapidly; AC lost nearly 50 lb. up to day 20 and BC lost 100 lb. up to day 40. Some of the body material lost may have been extra-cellular water, but most of it must have been tissue. Food consumption did not increase immediately lactation began so that a negative energy balance and loss of dry weight during at least the first part of this period of weight loss is certain.

The higher fat content of the milk during this entire period (Appendix Table 2) must also have contributed to the negative energy balance. The same pattern of weight loss and delayed response in food consumption during early lactation was observed by Nevens (1927) with his self-fed cows (cf. page 51). This pattern does not occur with the lactating rat (Figure 1), though the rat's lactation curve is probably different from the cow's, with a peak at the end rather than at the beginning of the lactation period.

Cow AC's weight loss would probably have ceased after about day 20 had food consumption not fallen. The additional 50 pounds lost after day 20 is obviously a part of the depression in body weight caused by the depression in food consumption between days 20 and 80. During the peak periods of consumption on either side of this depression AC clearly suffered greatly from indigestion. When food consumption fell below about 28 lb. a day she was quite comfortable again. The fact that none of the other cows, X, Y, or BC ever consumed more than 26 lb. a day and ever exhibited symptoms of indigestion also indicates that the occurrence of this condition was dependent upon the daily amount of food eaten. It is suggested that AC learned, and apparently tended to forget at intervals, that heavy eating was associated with great pain and so avoided the pain by eating less than she would have otherwise. Her food intake was thus limited during most of the first half of her lactation to a level (about 25 - 28 lb. a day) at which this pain could just be avoided.

The cause of AC's indigestion is not really evident. She

did exhibit symptoms identical to those described for 'acid indigestion' by Hungate, Dougherty, Bryant and Cello (1952), Myburgh and Quinn (1943) and Scarisbrick (1954). This condition frequently occurs in ruminants when they consume at one meal a large amount of starchy food to which they are not accustomed. The starch is rapidly fermented. Lactic acid accumulates in the reticulo-rumen and the concentration of volatile fatty acids decreases, indicating that lactic acid bacteria multiply more quickly than lactic acid fermenting species and that the latter are then suppressed by the low pH resulting from the accumulation of lactic acid. The pH falls below 5.0 and reticulo-ruminal motility is partially or completely inhibited. This state of affairs may persist for several days before normal conditions are restored, and during this time all the symptoms exhibited by AC are seen. Death results in a high proportion of untreated cases. An adapted animal consumes such starchy food every day in amounts which are lethal to unadapted animals. This is thought to result from a greater ability of the lactic acid fermenting organisms to cope with the rapid production of lactic acid and thus to prevent a fall in pH deleterious to themselves. Nevertheless, the same condition can apparently occur in even the adapted animal on occasion (Ndumbe, 1962; Nicholson and Cunningham, 1961). The way in which high reticulo-ruminal acidity and/or high lactic acid concentration causes discomfort and even death to the animal is unknown. The picture of reticulo-ruminal acidity obtained from AC suggests that high acidity was the cause of her distress. Though the pH values

found at times when she was distressed were not low, they were lower than found at times when she was not distressed. Moreover, the daily onset of the pain coincided with a sharp fall in pH of about 1 unit.

From day 80 to day 165 AC maintained a very stable weight, and clearly did so by gradually reducing her food intake from 28 to 24 lb. a day as milk yield declined. This weight was not further maintained after the end of lactation. Her patterns of weight gain and food consumption after lactation indicate that the latter variable was the independent one. The fact that the rate of weight gain continuously decreased up to the end of the experiment strongly suggests that AC would eventually have again reached a constant body weight. The patterns are strikingly like those presented by Kennedy (1950) for a rat in the development phase of hypothalamic obesity.

Cow BC maintained a constant body weight from day 60, following a brief depression associated with the depression in her food consumption, to day 220. She did this by reducing her food intake somewhat towards the end of her lactation as her milk yield declined and then by a further, marked reduction after she ceased lactating. After day 220 she increased in weight by 100 lb. and then settled down to an apparently new stable weight of about 1270 lb. This was her weight just after parturition and may have been a preferred weight for the conditions, but a much longer period of observation would have been necessary to adequately check this possibility.

It was assumed that cows X and Y could easily have consumed

more food than they did, even during periods of increasing body weight. This assumption was based upon the fact that AC and BC were able to comfortably consume 26 lb. of food a day when necessary. It was concluded, therefore, that food consumption was the dependent variable during periods of weight gain just as it obviously was when weight was stable - that X and Y regulated their food consumption in order to achieve "preferred" rates of weight gain as well as to achieve constant (and possibly preferred) body weights. The rates of gain preferred were not constant but changed from time to time. The evidence from AC and BC themselves for such preferred rates of weight gain is much stronger. Only with AC between days 190 and 210, when she was suffering from indigestion, was there any possibility that food consumption during a period of increasing body weight was the independent variable. The apparent constancy in the rate of dry-weight increase shown by BC before parturition and again between days 220 and 260 is striking.

The fact that the energy expenditure by AC and BC in the form of milk was far below their potentials, as judged from their previous farm production records (Table 2), needs comment. Their yields of 4 percent fat-corrected milk on Experiment 2 were no greater than those of their hay-consuming twins. With the latter, an inadequate energy intake was obviously the cause of this low production. This was not the case with AC and BC. Their production of fat-corrected milk was limited by a limiting rate of fat synthesis*, a limiting rate of energy expenditure rather than intake. The cause of this lowered rate of fat syn-

* The low energy content of the milk (and thus the low F.C.M. yield) was due to its low fat content.

thesis was an abnormal balance of necessary metabolites supplied to the udder, and this abnormal balance of metabolites was a result of the way in which the concentrate diet was fermented in the rumen (cf. page 99). A recent review by Rook (1961) deals with this problem in detail.

Cows AC and BC thus regulated their food consumption during the entire course of this experiment in order to achieve preferred rates of dry-weight gain and to maintain constant dry weights. They did lose some weight at the beginning of lactation because food consumption did not respond quickly enough to increased energy expenditure. Indeed, the initial (first 5-day) reaction of food consumption was to decrease. This is not, of course, surprising in view of the profound alterations in metabolism and in the pattern of hormone secretion brought about by parturition and the onset of lactation. No explanation can be offered for the fact that, after carefully maintaining constant dry weights throughout the latter half or two-thirds of their lactations and even after lactation, they then increased to apparently new constant dry weights. Whether or not they had or were about to have reached preferred dry weights at the end of the experiment is uncertain.

Cows AH and BH

AH and BH gained weight more slowly than their twins both before and after lactation. They suffered more prolonged periods of body weight loss and greater total losses during lactation. These differences were clearly the result of their lower energy intakes throughout the entire course of the

experiment. To equal their twins' net energy intakes AH and BH would have had to consume 36 lb. of hay daily before parturition and between 40 and 50 lb. a day during lactation, or 40 to 50 percent more than they were able to consume. Even after parturition AH would not have been able to match AC's average energy intake over the latter's post-lactation period.

It is concluded that food consumption was the independent variable throughout the entire course of the experiment. The weight gains that occurred before and after lactation were those permitted by food ingested in excess of that required for body maintenance. Only by regulating, i.e., restricting, energy expenditure (in the form of milk yield) during lactation were larger weight losses than did occur prevented. Evidence, to be discussed in the next section was obtained which supports the view that the increase in hay consumption observed at parturition was not a response to increased energy expenditure but rather to an increase in the capacity of the alimentary tract.

Rate of passage

Several modifications of the existing stained-food method of determing the rate of passage of undigested residues have been introduced in this study. Some of them may be useful in other studies as well. It has been shown that 12- and 24-h. faeces-collection intervals are adequate where the entire rate-of-passage curve (R value) is of interest. The more uniform particle-counting procedure allows particle counts to be

expressed on a fresh-faeces basis, thus eliminating the need to dry samples of faeces from each collection and the residue from each particle count. These two modifications eliminate much of the personal inconvenience and tedium of the method. It is thought that the precision of counting stained hay particles was increased by selecting only the hay stems for staining. The selection of stems is, however, a tedious job and their use may only be valid for comparative determinations with the same hay. The method has been successfully used to measure the rate of passage with animals with no fixed meal times and it has been established that residues of all food eaten during the day have the same rate of passage. The importance of selecting chemically related stains has been brought out.

The object of the rate of passage determinations was to obtain accurate estimates of 'C' which could then be used as an aid to interpreting the patterns of food consumption and body-weight change observed in Experiment 2.

The use of 'C' to correct body weight change

Dry weight was defined (page 25) as the weight of all the dry organic matter of the body, excluding only the indigestible dry organic matter of the alimentary tract.* For convenience, dry matter has been used as an index of dry weight. It is possible to use the change in the value of 'C' (alimentary

*In his experiments on the food consumption of cows, Lehmann (1941) termed indigestible organic matter "ballast," which term seem particularly apt in the present context.

content of indigestible dry matter) from one trial period to another to make a rough correction of simple body-weight change in order to improve its accuracy as an index of change in dry weight.

Between Trial 1 and Trial 2 the value of 'C' for cow BH increased by 8 lb. Therefore the loss of dry weight during lactation was really 8 lb. more than is indicated by the loss of body weight. Further, if this 8 lb. of indigestible dry matter was associated with about 7 times its own weight of water in the alimentary tract, a correction of 56 lb. is obtained. This is only true, of course, if the body retained extra water to maintain this 7 to 1 ratio and did not simply redistribute existing body water. Similarly, a correction of - 28 lb. may be applied to the body weight change from Trial 2 to Trial 3, and a slight negative correction also to the body-weight change of BC over the same period.

The differences in dry-weight change during lactation between twins of a pair was thus probably greater than is indicated by the differences in body-weight change; they may be as much as 50 lb. greater.

The use of 'C' in the interpretation of changes in hay consumption

Food consumption by cows AH, AC, BH and BC increased after parturition. Considerable evidence was obtained in this experiment which suggests that the cause of this increase was not the same for AH and BH on the hay diet as for AC and BC on the concentrate diet.

Makela (1956) observed an increase in hay consumption by cows after parturition. This increase occurred the very day after parturition. He argues that it could not have been a response to increased energy expenditure because it would not have been so rapid in that case. He considers that it was due simply to the fact that more space became available in the abdominal cavity and that this allowed a greater distention of the alimentary tract with ingested food;* the cows ate to physical capacity both before and after parturition. Reid (1961) found that consumption by ewes of hay or straw decreased in late pregnancy and that the extent of this reduction was greater in twin-bearing ewes than in those carrying single lambs. McDonald (1961) reported that in pregnant ewes normal spatial relationships among organs of the abdominal cavity are distorted during pregnancy, the abomasum being severely displaced in twin-bearing ewes. A compression of stomach compartments can be inferred from this. There is thus additional support for Makela's physical explanation of increased food consumption.

The balance of evidence obtained in Experiment 2 supports this physical explanation of the increase in hay consumption observed with cows AH and BH.

1) Cow AH's consumption during the 20 days immediately preceding parturition was 25 lb. a day; during the 20-day uniformity trial one month earlier she consumed 30 lb. a day. The

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*Paloheimo (1944) had earlier separated the compartments of the alimentary tract post mortem and found that they could all be stretched appreciably by very small increases in internal pressure; he suggested that the upper limit to the volume of ingesta the alimentary tract can contain is determined by the volume of free space in the abdominal cavity.

differences between the hays consumed in the two periods were not very great and would not have been expected to cause this 16-percent decrease in consumption. The rapid expansion of the pregnant uterus during this last month of pregnancy could have been responsible for this decrease.

2) The increase in food consumption after parturition was much more rapid with cows AH and BH than with their twins on the concentrate diet, occurring within the first 5-day period and even evident the following day (Appendix Table 2). This certainly suggests a response to changes other than in energy expenditure.

3) With cow BH the greater intake during lactation was accompanied by a greater value of 'C' and not by a smaller 'R' value. If 'C' is proportional to the alimentary content of total dry matter before and after parturition, a reasonable assumption since neither the digestibility coefficient nor the rate of passage was appreciably different between Trials 1 and 2, the greater intake of food was accompanied by an increased holding of digesting food dry matter and not by its more rapid passage out of the tract. This increment of food-holding capacity could either have been non-existent before parturition or simply unused. The former is more probable because the animal's food intake was quite clearly limited with respect to her energy requirement at that time. Her energy requirement was the amount of energy that would have permitted her to gain weight at her preferred rate, i.e., that rate at which BC gained during the same period, or the amount of net energy available from

about 36 lb. of hay a day. If physical capacity was thus limiting hay consumption before parturition, the deduced increment of capacity or space after parturition could not simply have been idle before, but must not have existed.

4) Cow BH's food consumption did not increase immediately after parturition to its highest level during lactation as did AH's; rather it increased in two distinct and equal steps 50 days apart. The increment of space occupied by ingested food dry matter after the second increase was either not completely utilised during the period between the first and second rise, or it was not totally existent at this time. Makela (1956) suggests that accumulations of fat in the abdominal cavity may have the same effect as the pregnant uterus in reducing hay consumption. Cow BH lost about 100 lb. during the period before the second rise in consumption and presumably some of this loss was of fat from the abdominal cavity. This would not, however, explain the sudden occurrence of the second rise; moreover, AH lost about the same amount of weight but her consumption remained constant from parturition to the end of the experiment. The former alternative does, by default, appear more probable, but no explanation for it can be offered. Cow BH's food consumption curve, in having a peak, conforms to that shown in Figure 2.

The increase in hay consumption by cows AH and BH was thus probably made possible by an increase in available space in the abdominal cavity. AC's and BC's consumption before parturition could not, of course, have been limited by physical capacity because the rate of passage of undigested dry matter increased

with the greater consumption after parturition, or in other words, C remains constant.

4. Conclusions and Their Significance

The experimental evidence obtained supports the hypothesis. The cows were able to regulate their food consumption on the concentrate diet to achieve preferred rates of increase in dry weight and stable weights under conditions of constant and variable energy expenditure. The lactating cows on the all-hay diet were prevented from so regulating their food consumption by the bulkiness of the hay; they had to rely on the regulation, i.e., restriction, of energy expenditure during lactation to maintain a minimum level of dry weight.

The data available from these experiments allow a limited, tentative description of this regulation of food consumption.

1) The degree of dry weight constanc achieved under constant rates of energy expenditure appears to be somewhat less, on a day-to-day basis, than is encountered with the human subject under similar circumstances (but with a greater variability in daily energy expenditure). The greater variability in daily body weight found for the cow may, however, reflect a less efficient maintenance of constancy of water content rather than of dry-weight.

2) Dry weights may be very large under sedentary conditions, as they are for other mammals; this suggests that with the regulation of food consumption by the cow also there is a non-responsive range of energy expenditure.

3) The response of food consumption to the increased energy expenditure of lactation shows a characteristic lag which causes a brief negative energy balance at the beginning of lactation.

Further studies, particularly long-term ones covering several years and several lactation cycles would provide the data with which to correct and amplify this description.

An obvious implication of these results is that now the cow must be reckoned with in the study of regulatory mechanisms, a study which has been pursued with only non-ruminant mammals to date. Any acceptable hypothesis about the nature of these regulatory mechanisms must take fully into account the differing chemical form in which the cow receives her digested energy and the accompanying differences in intermediary metabolism. The main problem raised would appear to centre around the identity of the circulating metabolite(s) which act upon the hypothalamic centres.* Mayer (1953c), for example, proposed that the availability of glucose, as indicated by aterio-venous blood glucose differences, is responsible for the short-term regulation of food consumption. Since, however, adult ruminants do not show appreciable arterio-venous blood glucose differences or any measurable diurinal variation of the existing differences (Reid, 1950), such a hypothesis would not appear adequate for the cow.

Though this has been a purely physiological study, it is interesting to note an example of the commercial significance the results have. In commercial dairying it is assumed that

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*Impressive evidence has been obtained by Larsson (1954) for a hypothalamic centre controlling the eating behaviour of the goat.

cows accumulate fat because they eat more than enough food to maintain energy equilibrium at a particular weight. This is the explanation given for the increase in weight of cows being "steamed up" before parturition and of those on good pasture late in lactation ("luxury consumption;" Crasemann, 1955). While this explanation is correct thermodynamically, the physiological explanation is obviously the reverse. Most non-lactating dairy cows endeavour to achieve preferred rates of increase in body weight. Owing to their relatively sedentary mode of life on the dairy farm, they tend to become quite heavy, even obese. The luxury consumption of grass is only the level of consumption required to achieve their preferred rates of body weight gain. Cows that are being steamed up eat all the limited food available to them in an attempt to attain their preferred rates of gain. It should be clear, therefore, that feeding standards are statements of thermodynamic facts and may provide a basis for economic decisions; they are not substitutes for physiological facts in the interpretation or prediction of cows' behaviour.

Summary

Six adult cows were used to test the hypothesis that cows, given free access to a concentrated food, regulate their food consumption, as do other mammals, to maintain constant body weights under conditions of constant and variable energy expenditure.

Two experiments were conducted. In Experiment 1 two dry, barren cows were kept under uniform management on an all-concentrate diet for 11 months. Daily food consumption and body weight were determined. During the first 3 months the cows increased in weight until they reached constant weights. Food consumption was higher when body weights were increasing than when they were constant. During the fourth month they were given walking exercise daily. They reacted to this with a marked reduction in food consumption and body weight; the treatment was imposed too quickly and they did not become adapted to it but became progressively more exhausted and lame. When the exercise was discontinued, body weights increased and again reached constant levels. As before the exercise, food consumption was higher when body weights were increasing than when they were constant. It is concluded that the animals regulated food intake (except during the exercise) to achieve preferred rates of increase in body weight and then to maintain constant weights.

In Experiment 2 two pairs of identical twin cows were kept under uniform management during the last 2-3 months of pregnancy, a 5-month lactation and a 2-5 month post-lactation period. One

of each pair was given an all-concentrate diet, the other an all-hay diet. Food consumption, body weight and milk yield were determined daily. The dry-matter digestibilities of the diets and the rates of passage of their undigested residues were determined with each cow before, during and after lactation. Body weights of the cows on the concentrate diet increased before lactation and remained constant during lactation. After lactation body weights remained constant or approached constant levels after periods of increase. Food consumption was higher during lactation than at other times and higher when body weights were increasing than when they were constant. The cows on the hay diet gained weight slowly before and after lactation and lost weight throughout most of their lactations. Their energy intakes were below those of their twins at all times when the latter were lactating or gaining weight. Their food consumption increased at parturition and did not decrease after lactation. The increases at parturition were not considered, on the basis of rate-of-passage and other data obtained, to be responses to the increased energy expenditures but to an increase in the physical capacity of the alimentary tract for ingested food. It is concluded that the animals on the concentrate diet regulated food intake to achieve preferred rates of increase in body weight and to maintain constant body weights. The cows on the all-hay diet were unable to so regulate their food consumption; because of the bulkiness of the hay, they were forced to consume at the limits of their physical capacity at all times even to achieve their inadequate energy intakes.

This experimental evidence is considered to support the hypothesis. Data obtained also permitted a tentative description of this regulation of food consumption. An example of the physiological and of the commercial significance of the conclusions are briefly discussed.

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Appendix

Table 1. Daily food consumption and body weight of cows X and Y in Experiment 1 and daily food consumption, body weight and milk production of cows AH, AC, BH and BC in Experiment 2. All values in pounds.

	Experiment 1				Experiment 2								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
-55					29			28¾						20½	1264	
54					27½			30¼						22¼	1272	
53					30¾			32½						18¼	1273	
52					23½			26¾						17¼	1284	
51					31½			34						23¼	1293	
50					30½			34½						21¾	1299	
49					25½			30¼						21¾	1304	
48					29¾			33¾						22½	1302	
47					31¾			35¾						21¼	1308	
46					31			31¾						20¼	1312	
45					33½			34½						23¼	1314	
44					29			28						22½	1320	
43					30¾			34						21¼	1322	
42					30¼			33¾						23	1351	
41					32¼			30						22¼	1335	
40					32½			33½			25¾	1281		21¾	1335	
39					28			29¼			24¾	1287		24¾	1340	
38					31½			29			25¾	1279		23¾	1348	
37											25	1275		23¾	1354	
36											27	1274		23¼	1364	
35											27	1282		21¼	1359	
34											25¾	1286		22¾	1361	
33											26¼	1286		23½	1365	
32											25¾	1292		22¼	1364	
31											24¼	1281		21½	-	
30								19	1225		25¾	1299		22½	1366	
29								16	1227		24¾	1299		23	1371	
28								18	1220		24½	1300		21¾	1372	
27								19	1210		24¾	1295		23¼	1378	
26								20¾	1215		26½	1299		21½	1380	
25					25¾	1231		22½	1213		23¼	1299		21¼	1390	
24					27½	1253		22½	1223		28	1299		18¼	1383	
23					26½	1258		20¼	1227		27	1304		23½	1379	
22					28¼	1260		13¾	1226		25½	1317		20	1393	

Uniformity Trial, days -60 to -42

Uniformity Trial, days -69 to -5

(continued)

	Experiment 1				Experiment 2								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
-21					26½	1261		15¼	1217		25¾	1319		20¾	1394	
20					25¾	1259		21¼	1224		27¼	1321		22	1389	
19					26¾	1263		20½	1226		29	1319		21¾	1393	
18					28½	1273		19¾	1235		26½	1322		23	1405	
17					27	1248		18	1228		29¾	1328		23¾	1417	
16					26½	1266		18	1238		18½	-		22½	1414	
15					26¼	1266		21	1234		32½	1313		20¼	1412	
14					25½	1260		18¼	1228		26¼	1316		20½	1416	
13					25¾	1278		22¼	1243		25½	1314		21½	1424	
12					26	1277		23½	1249		27¼	1319		22¼	1428	
11					24	1271		23	1237		25¾	1327		19¼	1419	
10					26¾	1267		19½	1235		-	1294		22¼	1433	
9					26¾	1263		22½	1251		28	1310		22	1439	
8					24½	1265		20¾	1270		28¾	1320		22	1438	
7					27	1269		21½	1276		26¾	1330		22¾	1448	
6					28¼	1280		20	1283		19¼	1311		22	1439	
5					26¾	1276		24	1283		25¼	1318		21½	1430	
4					24½	1287		22¾	1288		23¼	1312		21¾	1433	
3					24	1269		25	1288		24½	1316		-	-	
2					27¼	1266		26¼	1294		25	1320		19	1440	
1					29¼	1280		25	1302		27½	1338		17	1444	
parturition					20½	1128		16¼	1178		15¼	1173		18¾	1295	
1	17	1327	15¾	1189	31½	1141		23½	1181		28¼	1174		11¼	1257	
2	18¾	1335	16½	1197	34¾	1121		17¼	1167		28¾	1173		21½	1273	
3	19	1356	16¾	1215	34¾	1132	39½	22¾	1143	44½	30	1170	33	20½	1274	31½
4	15¼	1368	18¼	1218	31	1149	43	25½	1134	44½	28¾	1166	38½	21½	1266	35
5	16½	1356	18	1249	31¾	1118	41½	27¾	1144	47	28¾	1173	35½	21¾	1265	36
6	20¾	1362	18½	1229	32¾	1123	42	30	1120	49	31	1178	39	22½	1273	38½
7	20¾	1356	18¾	1223	36¼	1123	40½	29¾	1124	52	28¾	1170	39½	24¼	1255	40
8	12¼	1360	20	1228	31¼	1141	40	31¼	1114	54½	30½	1196	38	21½	1244	40
9	17½	1357	-	1214	35¼	1132	38	29½	1117	54	28	1184	38	19¾	1238	38
10	20	1354	17½	1219	26½	1099	30	28¾	1120	56½	29½	1194	37	22½	1238	41½
11	20¼	1365	14¼	1213	31	1141	39	30	1132	58	31	1174	40½	24½	1238	42
12	15	-	18¼	1217	31¾	1098	39	32	1137	59½	30¾	-	39	23½	1217	42½
13	21¾	1391	19¾	1262	35¼	1102	41	30¼	1126	61	28½	1158	39½	22½	1223	43½
14	23¼	1397	18	1232	31½	1099	39½	33¾	1122	58½	26½	1152	40½	23¼	1220	43
15	20¼	1398	15½	1229	29¾	1085	40	33¼	1143	63	31	1128	40	22¾	1210	44
16	25½	1402	21	1234	34½	1071	37½	32	1121	59	30¾	1128	39½	24¼	1204	45½
17	27	1410	16	1230	33¼	1095	36½	31¾	1131	65	33	1131	39	25¼	1204	47
18	25¼	1425	19¾	1242	31½	1086	38	33	1116	61	29¾	1120	41	25½	1198	46

(continued)

	Experiment 1							Experiment 2								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
19	21½	1396	20	1250	33	1085	39½	28	1106	59½	34¼	1125	41½	26¼	1202	50
20	21¾	1394	19	1258	33½	1076	39	26¾	1101	57	29	1132	39	25¾	1196	49
21	15¾	1390	16¾	1243	32¾	1080	34½	14¾	1076	49½	31	1138	38	26¾	1196	49
22	20¾	1409	16¼	1239	33½	1086	36½	17¾	1066	43½	32	1120	38	25¾	1182	50½
23	14¾	1406	21¼	1259	33½	1121	35	30¼	1085	50½	30¾	1118	38½	25¾	1194	51½
24	22¾	1416	23	1272	33¾	1083	39	31	1081	57	27	1098	37½	22¾	1195	46½
25	20¼	1414	20¾	1274	33¼	1092	38½	20½	1072	63½	-	1089	39½	24¾	1196	51
26	22¼	1420	18	1279	34¼	1084	40	26½	1064	53	-	1107	40½	21	1186	51½
27	17½	1415	20¼	1281	35¾	1089	36½	25¼	1064	61	-	1086	41	23¾	1186	49½
28	20¼	1430	21¼	1286	35¾	1097	38½	23½	1057	59½	-	1107	38	24	1164	51
29	17½	1429	17	1283	34¼	-	41	25¾	1061	54	30	1104	38	22¼	1181	49
30	22¼	1433	11¼	-	34	1088	44	24½	1070	60	29¼	1096	36	23¾	1171	49
31	24¾	1438	14	1268	31¾	1080	43	31½	1070	60½	29¾	1088	33½	18½	1160	50
32	17½	1419	15½	1266	36¾	1086	43½	26¾	1082	55	31¾	1074	35	22	1168	50
33	15	1447	13¼	1261	33	1074	43½	27½	1076	59	30¼	1092	33½	22	1160	49½
34	20	1434	7¾	1245	31¾	1074	42½	22	1059	59	29¾	1092	35	22¾	1150	52
35	16¼	1444	11½	1242	31½	1077	41½	30¾	1070	54½	31¾	1098	34	26	1175	48
36	25	1448	11¾	1252	31	1060	41½	25¼	1056	56	32¼	1088	36½	25	1176	39½
37	20	1452	16	1258	28½	1065	39½	24¾	1056	58	28¾	1066	35½	22¼	1168	50
38	20¼	1451	13½	1246	31¾	1070	43½	30	1056	56	32¾	1106	34	21¼	1164	47
39	19¼	1442	11¾	1270	35¼	1079	43	30½	1058	53½	30½	1090	36	20¾	1154	45
40	22¾	-	14¼	1261	31½	1068	42	29¾	1053	58½	29¼	1076	35½	19¼	1155	42
41	20¼	1456	9½	1262	31	1054	-	26½	1058	44	32½	1098	36	20½	1145	45
42	19½	1468	16½	1259	33	1052	44	29	1057	55½	31½	1102	36	16½	1135	43½
43	24¾	1464	10¾	1251	35¼	1051	45½	26	1064	51½	28½	1070	39½	19	1127	41½
44	17¼	1441	14½	1247	33¼	1050	43	27¼	1053	54	32	1097	34½	16¾	1114	44
45	20¼	1461	16¾	1263	31¾	1047	43	31	1060	55½	29¼	1094	37	16¾	1119	41
46	14¼	1454	6¾	1257	33¾	1054	44	28	1060	53	31¾	1089	35	18	1109	42
47	16¾	1465	8	1265	34½	1055	41½	28	1077	55	33¼	1107	36	18¾	1108	40½
48	18¾	1439	13	1258	31¾	1052	42	28¼	1064	48	33	1089	35½	22½	1104	43
49	17	1441	17¼	1263	34	1047	43½	14¾	1035	54	33	1076	39½	20¾	1116	44
50	12½	1444	11¾	1234	34¼	1046	42	26½	1049	46½	35½	1084	42	19	1116	44
51	18¾	1453	14¾	1235	34½	1052	40	20¼	1049	44½	35½	1058	40½	21¾	1122	45½
52	16¾	1452	6½	1232	33	1056	42	30	1044	48½	36¾	1071	39½	22	1128	46
53	-	1416	11¼	1232	32¾	1044	42½	28¼	1057	50½	34	1082	39	24½	1126	47
54	21¼	1449	9¼	1226	31½	1036	39½	25¼	1050	49	36½	1082	38½	26¾	1133	49
55	17½	1443	11¼	1218	32	1060	41½	25	1054	46½	32½	1070	38½	26¾	1140	47½
56	21½	1456	11	1234	29½	1036	39½	26	1060	48	35¼	1058	39½	25	1138	47
57	20½	1456	10¾	1226	32½	1035	37½	27½	1071	47	34	1074	38½	25	-	48½
58	19¾	1469	8½	1241	30½	1040	39½	24¾	1066	47½	33¾	1060	38½	24¼	1137	48

(continued)

	Experiment 1							Experiment 2								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
59	22¼	1481	12¼	1246	30¾	1040	38	29¼	1083	45½	34¾	1071	38	26	1158	48
60	19½	1476	13¼	1261	31½	1033	39	18½	1065	45	36½	1072	38½	23½	1145	48½
61	19	1492	10	1242	31¾	1039	37	22	1057	42	34¼	1059	35½	22½	1142	46½
62	19¼	1498	12¼	1249	31¼	1030	39	26½	1046	43	33	1068	35½	23¾	1132	46½
63	22¾	1494	11½	1240	32¾	1043	37½	24½	1050	44½	37¼	1078	36	25¾	1132	46½
64	21½	1496	9½	1229	31½	1042	38	27¼	1062	41	35¼	1098	35	24¾	1136	47
65	23	1507	14	1241	34½	1048	41	23½	1057	43	31½	1080	33	27	1149	47½
66	16¾	1499	10¾	1239	35	1054	36½	24¾	1059	43	32¾	1062	39	26¼	1152	48½
67	20½	1497	15¼	1259	33	1060	36½	25½	1064	38½	38	1078	35½	24½	1132	48
68	20½	1502	16	1265	30¾	1058	35	27	1081	40½	33¼	1072	37	28¼	1150	46½
69	18	1502	1¾	1258	31½	1043	36½	25	1084	40	33¼	1072	36½	25¼	1143	49½
70	21	1510	7¾	1262	33½	1052	32½	16¾	1056	44	31¾	1062	38	21¼	1140	47
71	15½	1482	10	1242	35	1050	32½	24¼	1056	38½	31¾	1062	35½	22	1134	46½
72	20½	1506	10	1230	32½	1038	36½	29½	1084	41	37½	-	36	27¼	1126	45½
73	17½	1476	8¼	1228	32¼	1043	34½	30¾	1074	45	35½	1078	35	25½	1126	46½
74	18	1456	9½	1226	34¼	1030	31½	30	1079	42½	35¼	1084	37	24¼	1148	44
75	17¼	1485	10¼	1234	29	1034	37½	30¾	1096	44½	32¾	1036	33	24	1127	48½
76	15¼	1487	11	1242	33¼	1032	35	29¾	1088	46	32¼	1050	35½	25¼	1156	42
77	13¼	1488	11½	1243	35¾	1049	35½	31½	1102	45	36¾	1050	36	20¾	1160	43½
78	18¼	1503	12½	1243	30	1022	33	30¾	1094	51	35¾	1060	35½	21	1142	45
79	20½	1498	10¾	1231	32	1038	32	32¾	1100	47½	36	1058	34½	26¼	1140	45½
80	21¼	1500	8	1244	29¾	1034	32	30¼	1097	45½	36¼	1067	33	26¼	1138	46
81	19	1482	13½	1233	33¼	1032	29	29	-	46	34¼	1066	34	25¼	1152	44
82	17½	1486	11	1248	36	1034	32	25½	1088	46½	36¼	1062	32	26	1156	45
83	19½	1510	12¾	1246	34½	1032	33	31	1092	44½	34½	1062	33	26	1162	44½
84	18	1501	10¾	1234	29	1018	32	29	1082	46	33¾	1066	34	27	1124	44
85	19¾	1499	5	1232	34¼	1036	32½	29	1094	48½	34¾	1042	32½	24½	1142	43
86	17½	1490	14½	1264	33½	1028	33	28¾	1084	46	34¾	1056	32½	23½	1138	44
87	12¼	1506	11½	1252	36	1034	33	20½	1090	46½	32	1038	32½	23½	1134	42½
88	21¼	1520	9	1240	32¾	1036	33	26½	1086	42½	33	1018	32½	26½	1150	41
89	20	1501	14¼	1256	31¼	-	30	31¾	1103	40½	34¼	1038	32	23	1150	44½
90	19½	1508	8½	-	33½	1024	30½	20	1093	43	36½	1043	33	23¼	1164	42½
91	18	1460	9¼	1246	34¼	1038	31	28¾	1096	41½	34¼	1050	31½	17¼	1140	40
92	15½	1472	14¼	1244	33	1026	31½	28½	1082	46½	33	1046	31½	24½	1144	44
93	4¾	1466	9½	1234	33¼	1026	32	29	1096	47½	35½	1050	30½	19¼	1150	41½
94	20¼	1486	9½	1238	33½	1022	35	26½	1084	44	33	1028	31	22¼	1158	39
95	15¾	1476	4½	1212	34¾	1018	30	26¾	1086	43½	34	1032	29	25¾	1142	41
96	11¾	1464	2¾	1216	32½	1018	33	28	1088	44	33	1064	28½	20¾	1144	42
97	17½	1468	8	1194	35½	1025	33	28	1090	45½	33½	1064	30	22½	1166	42

(continued)

	Experiment 1							Experiment 2.								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
98	6¾	1444	11¼	1187	33½	1024	30½	26½	1094	42	34	1056	30	23¾	1180	42
99	19¾	1479	3¾	1193	31	1020	30½	-	1095	43	35	1036	31	24¾	1162	41
100	16½	-	4½	1180	33½	1022	31	26¾	1098	44	35¼	1058	29	27	1142	44
101	16¾	1446	3½	1174	35½	1038	32	26¼	1106	38	34¼	1040	30	25¼	1152	40
102	15½	1456	5¼	1183	31½	1020	30½	27¼	1108	44	36	1040	28½	23½	1156	40
103	10¾	1442	3	1170	34	1020	30½	27¼	1088	44½	33¾	1050	30	24	1154	42
104	17	1480	5¼	1170	34	1020	30½	28½	1100	40½	32	1030	27½	17	1176	38½
105	15½	1455	4½	1170	35	1022	31½	27	1112	43½	35	1058	27	23¼	1160	38½
106	14	1442	8	1176	32¾	1040	29	28	1108	40	29½	1028	30	22½	1174	38
107	11½	1438	¼	1150	32¼	1021	31½	29	1108	39	34½	1028	25	22	1124	39½
108	17¾	1447	6¾	1151	33¾	1028	31	30	1084	45½	36½	1042	30	23¼	1150	38
109	14	1436	3¾	1146	32½	1038	27	27¼	1110	43	32¼	1050	25½	22	1132	38
110	10	1410	1¾	1130	33	1030	30	25¼	1106	42	34¾	1050	30	21	1166	38
111	1¾	1396	½	1144	33½	1016	33	25¾	1102	43	32½	1046	27½	23¼	1184	37
112	1½	1384	1¼	1128	35	1022	29	27	1112	44½	32½	1042	29	22¾	1142	40
113	10½	1384	1¼	1112	33½	1016	29	26¼	1096	42½	27¼	994	26	20¾	1149	37½
114	2½	1362	1¼	1116	32¾	1026	29	24½	1098	45	33½	1030	28	21¾	1146	38½
115	2½	1354	1	1116	35	1022	33	27½	1098	41½	31¼	1056	28	23½	1145	37
116	2½	1332	1¾	1106	34½	1012	29	23¾	1100	42	34¾	1044	26½	24	1165	35
117	3	1328	1½	1112	34	1028	31	25¼	1113	41	31¾	1028	27	22½	1158	36
118	5¼	1337	1	1114	31½	1008	29	22½	1108	41½	32¾	1068	26½	23½	1156	35½
119	4¼	1330	1¼	1106	34½	1014	29	20¼	1092	41½	34¼	1062	26½	21	1166	35
120	1¾	1328	1	-	34¼	1018	31	26¾	1114	41	33¼	1050	25	24½	1158	33
121	5	1332	1¾	-	33½	1004	30½	23½	1106	40	32¼	1054	24	24¾	1160	35½
122	5½	1342	1¼	-	33¾	1010	28	25¼	1116	41½	32¾	1052	27½	24¾	1174	33½
123	5¾	1354	¾	1090	31½	1015	31	25½	1114	41	33	1047	25	23½	1174	37
124	9¾	1344	¾	1088	33¾	1028	28	23¼	1104	39½	35½	1054	25	25¼	1152	35
125	12¼	1336	3	1086	31	1020	27	24	1102	39	29½	1032	28	25¾	1169	36
126	11¼	1334	2¼	1085	32	1020	28	27¼	1092	39½	32¾	1028	26½	24¼	1174	37
127	13	1337	½	1087	32½	1014	30½	24	1112	38	34	1013	26	21¾	1166	40
128	10½	1352	4¼	1076	32½	1034	27	26½	1104	38½	36	1030	27	24½	1163	33
129	14	1362	1½	1070	32½	1034	27½	27¼	1098	37	35¾	1050	26½	22¼	1158	32
130	14½	1366	2¼	1066	32½	1016	29	26½	1092	40½	34¾	1038	26	23¾	1156	33
131	14	1358	5½	1080	32¾	1002	30	24½	1112	34	30½	1037	26	23¾	1170	33½
132	13½	1348	5½	1074	31¼	986	28½	25¾	1106	40½	32	1038	26½	24	1178	34
133	14	1354	1½	1074	32½	982	27½	27¼	1106	42½	33¼	1032	26	23	1184	33½
134	13¾	1360	5½	1082	32¾	1000	26	27½	1110	40	34½	1044	25½	23	1164	33
135	14	1350	6½	1074	29¾	992	27	24	1098	37	30¾	1038	25½	26½	1165	29
136	13½	1364	7½	109⁰	34	1002	28½	27	1098	40	34½	1056	24	23½	1158	32
137	11	1354	9¼	1100	32½	1004	25	27½	1092	44	31¾	1050	23	23¼	1158	30

(continued)

	Experiment 1.							Experiment 2.								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
138	15	1372	0-	1086	34¼	1006	26½	28	1088	40	33	1060	25	21½	1173	33
139	14¼	1368	2½	1090	27¼	1008	18½	25¼	1088	39	34¾	1096	25	20	1180	29
140	12¾	1366	9¾	1090	29	998	33½	25½	1088	40	34¾	1065	23½	22½	1170	29
141	15½	1382	7½	1086	31½	994	25	23	1092	37	34¼	1062	25	18¾	1168	30
142	13¼	1364	8¼	1094	32¾	986	27	18½	1088	36½	31¾	1050	24	22½	1160	28½
143	13¾	1368	10½	1084	31	992	25	27	1100	37	29¾	1041	25	22¾	1157	30
144	14½	1376	2¼	1082	29¼	1006	28	25	1084	36½	33¾	1054	23½	17¾	1166	29½
145	14¼	1376	0-	1090	34	991	26	23½	1074	35½	35¾	1053	24	18	1148	26
146	16½	1396	10¾	1083	30¼	984	24	23¾	1084	37½	31	1042	24	21	1137	31
147	14¾	1396	11¼	1086	31¾	982	25½	27¼	1082	38	29¼	1048	25	15¼	1128	29
148	16¾	1410	10¾	1102	31	997	24½	25	1086	38½	31¾	1041	25	20¾	1131	29½
149	15¾	1424	8½	1097	31	1004	29	26¼	1093	39	30¼	1041	25½	18¾	1143	30
150	15¾	1406	10¼	1122	30¼	996	25	26¼	1112	39	36	1049	25	17½	1140	29
151	14¼	1384	12¾	1120	35	1014	25	21¼	1089	38	31¼	1055	20	21¾	1142	24½
152	12	1382	13¼	1120	33½	1004	25	27¼	1101	36	36	1072	-	21	1152	23
153	14	1376	8½	1120	32	1008	25½	23¾	1101	35	31½	1072	18	19	1168	-
154	12	1376	14	1136	30¾	1008	25½	24	1099	36	36¼	1087	-	18	1146	25½
155	16¾	1392	14¼	1136	36	1010	27½	22	1102	38	36¾	1096	15	21½	1170	
156	14¼	1379	15	1140	32½	1002	26	22¼	1092	36	32¼	1095		22½	1188	
157	15½	1374	15¼	1129	35	1019	26½	27	1107	37	35¼	1096		18¾	1179	
158	12	1382	13¼	1142	33½	1032	25	25½	1114	33	33¼	1092		15	1166	
159	14½	1397	14¾	1146	33¾	1013	26½	27½	1108	36½	36¾	1105		18½	1161	
160	9	1368	16¼	1158	32½	1003	26	26	1099	35	35¾	1099		15¾	1167	
161	15¾	1382	13	1132	32¼	1006	18	23¾	1086	37½	36	1108		15¾	1170	
162	17¾	1416	13½	1142	30	987	32	24¾	1083	38	32½	1102		13½	1169	
163	16½	1404	17	1146	33¼	1001	24½	22	1104	35	32¼	1095		10¾	1146	
164	17¼	1394	15	1150	28¼	1006	25½	20¾	1090	38	33	1100		8½	1140	
165	13¾	1386	16¾	1160	33	1006	23	23¾	1098	36	32½	1090		12	1132	
166	15¼	1397	16½	1162	34¼	1008	19	10	1096	31	34	1086		12	1130	
167	19	1420	13¼	1168	34½	990	-	15	1081	22	31½	1089		11¼	1106	
168	16½	1436	18¼	1188	29¼	1004	20½	15	1076	22	32¾	1096		11½	1126	
169	18½	1436	19¼	1173	34½	1028	-	15	1059	25	32	1100		14¼	1144	
170	17¾	1436	20¼	1176	32¼	1029	11	25	1103	-	32	1099		17½	1152	
171	15¼	1435	20½	1187	35	1052	-	27½	1089	36½	34½	1100		20¾	1156	
172	14¼	1424	18	1197	31¼	1050	-	20	1106	-	33¾	1113		18¾	1164	
173	6	1420	18¾	1194	31¾	1032	15	15¼	1093	24½	36¾	1085		17	1166	
174	15½	1431	10	1189	36	1053	-	26¼	1110	-	38	1093		16¾	1166	
175	16½	1420	22	1200	31½	1043	-	23½	1072	19	39	1120		19	1168	
176	19½	1448	16¾	1195	35¾	1061		23	1100	-	33¼	1118		18	1168	
177	21¼	1437	17¾	1173	31¾	1057		22¾	1140	-	33¾	1128		19¼	1179	

(continued)

	Experiment 1						Experiment 2								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC	
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
178	21	1419	13	1164	34	1063		19½	1100	32	31½	1114		16¼	1178	
179	18½	1443	15¾	1162	31½	1069		26¼	1127	-	36¾	1114		20¼	1185	
180	16¾	1435	17	1170	32¼	1058		28	1149	-	35	1114		16¾	1176	
181	18¼	1463	13	1147	28	1058		29	1172		33¾	1132		18¼	1180	
182	18¼	1440	15¾	1150	29¼	1048		22¼	1151		30½	1090		17¾	1166	
183	11¾	1432	15½	1160	32½	1010		27½	1146		30¼	1088		16¾	1170	
184	1¼	1420	10¾	1154	28¾	1023		25¼	1167		-	-		15¼	1177	
185	5	1432	13¾	1159	29¼	1016		25½	1165		-	-		17¾	1175	
186	18¼	1440	10¾	1144	31½	1048		28¼	1182		33	1100		15¼	1172	
187	17	1436	10¾	1168	33	1048		29¼	1166		26½	1100		17	1162	
188	0	1414	15	1155	31	1047		30	1172		35½	1122		15	1161	
189	0	1417	13½	1147	33¾	1049		30¾	1192		33½	1126		13½	1164	
190	5¾	1408	13	1152	36¼	1049		31	1206		30¾	1134		15	1161	
191	19	1448	12¼	1155	31¾	1044		28¾	1190		35¼	1129		17¾	1165	
192	16¾	1410	16½	1156	31¾	1065		29	1200		37	1144		16¾	1164	
193	11	1398	17½	1162	31½	1062		30¼	1204		32¾	1124		16½	1152	
194	18	1398	4	1154	30½	1075		27¼	1218		31½	1117		17	1178	
195	14¼	1415	16	1179	30	1060		27½	1214		30¼	1135		15¼	1154	
196	18¾	1432	11¼	1146	33	1078		26½	1212		35½	1134		18½	1164	
197	17¼	1436	18¼	1125	32½	1079		26	1229		35¼	1136		18¾	1164	
198	18	1435	11¾	1141	30¾	1075		28	1225		30¼	1124		14½	1154	
199	16	1438	9	1149	31½	1072		26¼	1248		33¾	1135		17¼	1150	
200	11¼	1413	9¼	1137	34¾	1082		25	1240		33½	1120		15¾	1152	
201	15½	1420	13½	1152	34¼	1086		24½	1234		34¼	1134		17	1152	
202	19¾	1428	16½	1164	32	1078		24¾	1221		32¼	1140		17	1156	
203	20¼	1434	12¼	1160	36½	1076		27¾	1227		35	1152		17	1164	
204	2	1394	13¾	1165	-	-		25¾	1250		32¾	1138		16¾	1155	
205	20	1439	16¾	1160	36¾	1091		28	1230		29¾	1123		14½	1156	
206	17¾	1426	12	1155	34	1090		27½	1228		30½	1119		16¾	1149	
207	19¼	1415	16¾	1160	31	1096		28¾	1233		34	1136		15	1164	
208	11	1398	14	1157	29¾	1085		28½	1242		36	1160		14¼	1144	
209	15¾	1412	12½	1170	35½	1094		27½	1222					15¾	1156	
210	6½	1392	12¼	1145	32½	1085		24¾	1230					13¾	1160	
211	8½	1388	7½	1157	33½	1097		27¾	1230					15	1157	
212	21¾	1424	8¼	1123	33¾	1116		29¾	1231					16¼	1148	
213	9	1418	17½	1172	30¾	1096		30½	1235					17¼	1144	
214	14½	1421	4	1162	33½	1090		28	1236					15	1134	
215	18	1420	14¼	1168	34	1096		30¼	1233					17¼	1146	
216	18	1416	12	1152	32	1095		28¾	1247					16	1147	
217	16¾	1415	3½	1140	32	1101		25¼	1242					16½	1158	

(continued)

	Experiment 1							Experiment 2							
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
218	21	1449	12½	1156	32½	1088		28	1260					16	1144	
219	17½	1470	17¾	1149	32¼	1092		28¼	1250					15½	1150	
220	26	1460	12¾	1157	32¼	1096		27¼	1252					17	1156	
221	6½	1444	11½	1161	29¾	1081		26	1270					16¼	1155	
222	20	1444	12¼	1149	27¼	1087		26½	1270					15¼	1160	
223	19½	1438	10¾	1140	27¼	1089		25	1284					18¼	1156	
224	16¼	1440	13½	1147	30¾	1092		27¾	1296					17½	1156	
225	20¼	1430	10½	1133	28½	1102		24¼	1276					18	1166	
226	19¾	1437	6	1164				22¼	1272					19¼	1167	
227	17¾	1435	4½	1152				27¼	1278					18½	1168	
228	16½	1432	11	1200				26½	1280					18½	1184	
229	14½	1434	9¼	1188				27¼	1282					15	1174	
230	13½	1434	14¾	1178				28½	1278					16¼	1167	
231	18¾	1452	14	1164				24	1286					17½	1178	
232	19	1444	11¾	1162				25	1284					15	1172	
233	10	1427	10¾	1172				22¾	1286					17½	1179	
234	18½	1450	16	1158				25	1288					18¼	1184	
235	18	1446	11½	1172				23	1291					18½	1174	
236	12¾	1450	16½	1183				26¾	1286					18¾	1186	
237	15	1446	13¾	1168				26½	1274					18	1180	
238	11½	1436	13¼	1160				27½	1274					18	1207	
239	20¼	1446	14½	1157				25¼	1292					18½	1203	
240	21¾	1476	17½	1184				27	1299					19½	1210	
241	18¾	1472	16	1184				27	1286					19¼	1206	
242	19¼	1472	13¾	1180				24	1308					18¾	-	
243	21¾	1488	15	1176				26	1306					17¾	1226	
244	18¼	1472	13	1170				27¼	1324					19	1215	
245	17¼	1470	14¾	1172				25¼	1314					19½	1226	
246	18	1480	16	1182				29	1324					20	1222	
247	21¼	1455	14¼	1186				27¾	1326					19	1222	
248	19	1458	16½	1180				23	1328					18½	1241	
249	19¾	1473	15½	1178				22	1317					18¾	1236	
250	19	1462	17	1180				28	1316					19¼	1232	
251	22¼	1455	15½	1196				23¾	1324					19¼	1225	
252	20¼	1474	16¼	1192				25½	1336					18¼	1222	
253	23	1478	14¾	1199				20¼	1322					20½	1225	
254	21½	1500	17½	1198				26	1338					20¾	1232	
255	21	1486	17½	1204				25¾	1318					19¼	1243	
256	18½	1490	11½	1182				27¾	1320					19¾	1245	
257	18	1456	17½	1186				28¼	1316					19¼	1252	

(continued)

	Experiment 1							Experiment 2							
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC	
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt. Milk
258	16 1/4	1464	13	1198	.			25	1342					19 1/4	1250
259	17 1/2	1481	5 3/4	1165				23 1/2	1342					17 1/2	1258
260	18 3/4	1458	10 1/2	1186				27 1/4	1348					19	1260
261	17	1476	12 3/4	1198				24	1338					18 1/2	1263
262	20 1/2	1450	18 3/4	1209				22 1/2	1344					18	1264
263	15 1/4	1486	16	1190				25	1340					16 3/4	1258
264	17	1481	17	1194				25	1346					15 1/4	1266
265	16 1/4	1484	18 3/4	1208				22 1/2	1344					17	1270
266	18 3/4	1458	18 1/4	-				26 1/4	1332					17 1/4	1268
267	14 1/2	1486	16 3/4	1206				19 1/2	1339					15 1/2	1256
268	20 1/4	1459	15 1/4	1200				24	1344					18 1/4	1264
269	15 3/4	1458	9 1/4	1214				26	1350					16 1/4	1276
270	16 1/2	1439	19 1/2	1216				19	1340					17	1281
271	20 3/4	1452	16 1/2	1203				22 1/2	1328					17 1/4	1273
272	17 1/4	1467	19 1/4	1204				22 3/4	1341					17 1/4	1259
273	13 3/4	1470	16	1210				22	1347					17 1/2	1252
274	14 1/4	1460	15 1/4	1209				24	1346					17 1/4	1246
275	13 3/4	1460	7 3/4	1210				23 3/4	1356					15 3/4	1266
276	7 1/4	1445	14 1/4	1219				21 1/4	1366					16 1/4	1274
277	14 1/4	1444	13 1/2	1212				25 1/2	1364					16	1263
278	19 3/4	1448	12 1/2	1212				20 1/2	1362					16 3/4	1261
279	17 1/4	1458	19 1/2	1204				18	1365					16 3/4	1250
280	15 1/2	1460	15 3/4	1190				22	1365					18 1/4	1247
281	20 1/2	1481	15 1/4	1204				21 3/4	1370					18	1263
282	8 1/4	1468	17	1231				21 3/4	1372					16 1/2	1258
283	17 1/4	1458	16 1/2	1227				19	1369					13	1250
284	7	1486	14 1/2	1206				22 3/4	1372					12 1/4	1237
285	16 1/4	1507	10 3/4	1206				22 3/4	1374					13 1/2	1253
286	18 1/2	1504	18 3/4	1214				20 1/4	1362					10 1/4	1250
287	18 1/4	1464	16 1/2	1204				21	1376					10 3/4	1253
288	10 3/4	1472	17 3/4	1206				22 3/4	1387					17 1/2	1265
289	20 3/4	1468	19 1/4	1204				23 1/4	1374					12 3/4	1262
290	19	1450	20 3/4	1220				23 3/4	1372					15 3/4	1272
291	10 1/4	1450	20 3/4	1238				23 1/2	1376					13 3/4	1272
292	14 3/4	1466	20 3/4	1244				23	1369					17	1268
293	2 1/4	1458	17 3/4	1261				20 1/2	1368					15 1/4	1262
294	9	1465	21	1264				23 1/2	1367					16 3/4	1270
295	15	1483	19	1254				21 3/4	1383					17	1264
296	20 1/2	1467	18 3/4	1248				22 1/4	1388					14 1/2	1248
297	19	1466	18	1255				22 3/4	1365					15 1/2	1280
298	17 1/4	1458	19	1260				22	1388					15 1/4	1278

	Experiment 1							Experiment 2								
	Cow X		Cow Y		Cow AH			Cow AC			Cow BH			Cow BC		
Day	Food	Wt.	Food	Wt.	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk	Food	Wt.	Milk
299	19¼	1470	18	1252				22¼	1378					14½	1277	
300	18	1460	17½	1244				21¾	1378					17¼	1280	
301	12	1475	16	1244				21½	1364					17	1283	
302	19¾	1482	18¾	1240				19¾	1367					16¼	1288	
303	18¼	1495	11¼	1269				23¼	1384					15¾	1278	
304	12¾	1475	20¾	1272				23½	1391					17½	1284	
305	11	1486	19½	1254				24	1393					16¾	1286	
306	8	1454	19¼	1250				20½	1396							
307	13¾	1496	16½	1242				21¾	1414							
308	13¾	1479	18½	1234				20	1402							
309	18¾	1482	17¾	1242				22¼	1406							
310	16¼	1482	14¾	1226				22½	1400							
311	18½	1485	17	1233				23¼	1399							
312	15	1489	16¾	1220				24¼	1397							
313	17¼	1480	19½	1240				23	1410							
314	18¼	1496	12	1237				22¾	1434							
315	19¾	1478	16½	1238				20¼	1420							
316	17½	1460	15¾	1240				21	1406							
317	19½	1496	16¾	1249				21¾	1408							
318	20	1480	17¼	1256				23¼	1416							
319	16½	1482	16¼	1252				24	1416							
320	20¾	1485	14	1270				21	1410							
321	18½	1493						22	1412							
322	14¼	1473						20½	1408							
323	16¾	1480						20½	1412							
324	2¾	1478						22¾	1415							
325	19½	1472						22½	1410							
326	17½	1491						19¾	1422							
327	10	1477						19¾	1410							
328	11	1482						20	1412							
329	13¾	1482						21½	1418							
330	13½	1474						21¼	1425							

Table 2. Milk Composition.

Cow AH

Day	Fat	S.NF.	C.P.	Lact.
16	4.52	9.00		
37	4.40	8.44	2.90	4.62
43	3.76	8.14	2.87	4.66
49	3.88	8.15	3.00	4.74
58	3.88	8.34	2.85	4.74
64	3.05	8.09	2.88	4.56
70	3.66	8.03	2.89	4.48
77	4.69	8.05	3.09	4.50
84	3.44	8.11	3.13	4.68
91	5.17	7.93	3.00	4.43
98	3.40	8.31	3.10	4.67
107	2.69	8.25	3.16	4.56
112	4.08	8.13	3.13	4.52
119	3.85	8.34	3.15	4.69
126	4.41	8.19	3.14	4.39
133	5.00	8.19	3.15	4.75
140	4.22	8.13	3.21	4.42
147	3.00	8.27	3.13	4.71

Cow AC

Day	Fat	S.N.F.	C.P.	Lact.
8	4.48	9.94	-	-
29	2.56	8.88	3.08	5.02
35	1.81	8.69	3.02	5.09
41	1.79	8.86	3.13	5.08
50	2.25	8.77	3.15	4.93
56	1.49	8.86	3.01	4.94
62	2.10	8.53	2.96	4.81
69	1.47	8.74	3.10	4.80
76	1.40	9.22	3.64	4.99
83	1.88	8.98	3.39	4.84
90	1.95	8.91	3.34	4.97
99	1.38	9.10	3.51	-
104	1.68	8.79	3.43	4.74
111	1.77	8.91	3.46	4.76
118	1.70	9.05	3.47	4.76
125	1.40	8.88	3.36	4.99
132	1.64	8.87	3.26	4.93
139	1.69	8.94	3.33	4.77
146	1.50	8.68	3.15	4.77

Cow BH

20	4.93	8.94	3.24	5.02
26	4.07	9.11	3.19	5.45
32	4.16	8.79	3.21	5.10
41	5.31	8.75	2.92	5.01
47	4.40	8.72	2.95	5.13
53	3.70	8.61	2.99	4.83
60	3.59	8.32	2.95	4.78
67	3.79	8.37	3.15	4.91
74	3.30	8.77	3.14	5.21
81	3.14	8.50	3.13	4.82
90	3.83	8.42	3.12	4.85
95	3.70	8.74	3.26	5.11
102	2.98	8.51	3.14	4.89
109	3.88	8.60	3.16	4.80
116	3.75	8.67	3.13	5.18
123	3.98	8.38	3.16	4.71
130	3.27	8.70	3.24	4.98
137	3.03	8.51	3.23	4.93
144	3.23	8.48	3.16	4.71
151	3.22	8.57	3.30	4.92

Cow BC

5	4.50	9.95	4.75	4.39
11	3.79	9.36	3.76	4.98
17	3.09	9.24	3.46	5.09
26	2.83	9.07	3.18	5.11
32	2.72	9.14	3.20	5.16
38	2.06	9.03	3.10	5.03
45	3.06	8.43	2.76	4.84
52	2.24	9.09	3.40	5.15
59	1.74	9.24	3.35	5.33
66	1.72	9.18	3.24	5.13
75	1.70	9.24	3.36	5.15
80	1.74	9.01	3.36	5.03
87	1.89	8.98	3.44	4.98
94	1.63	-	3.32	4.86
101	1.91	9.38	3.41	5.27
108	2.53	9.19	3.42	4.98
115	1.78	9.20	3.47	4.93
122	2.10	9.03	3.37	4.94
129	1.62	9.13	3.45	4.80
136	2.09	9.07	3.47	4.96
145	2.30	8.77	3.51	4.74
151	2.14	8.93	3.43	4.63